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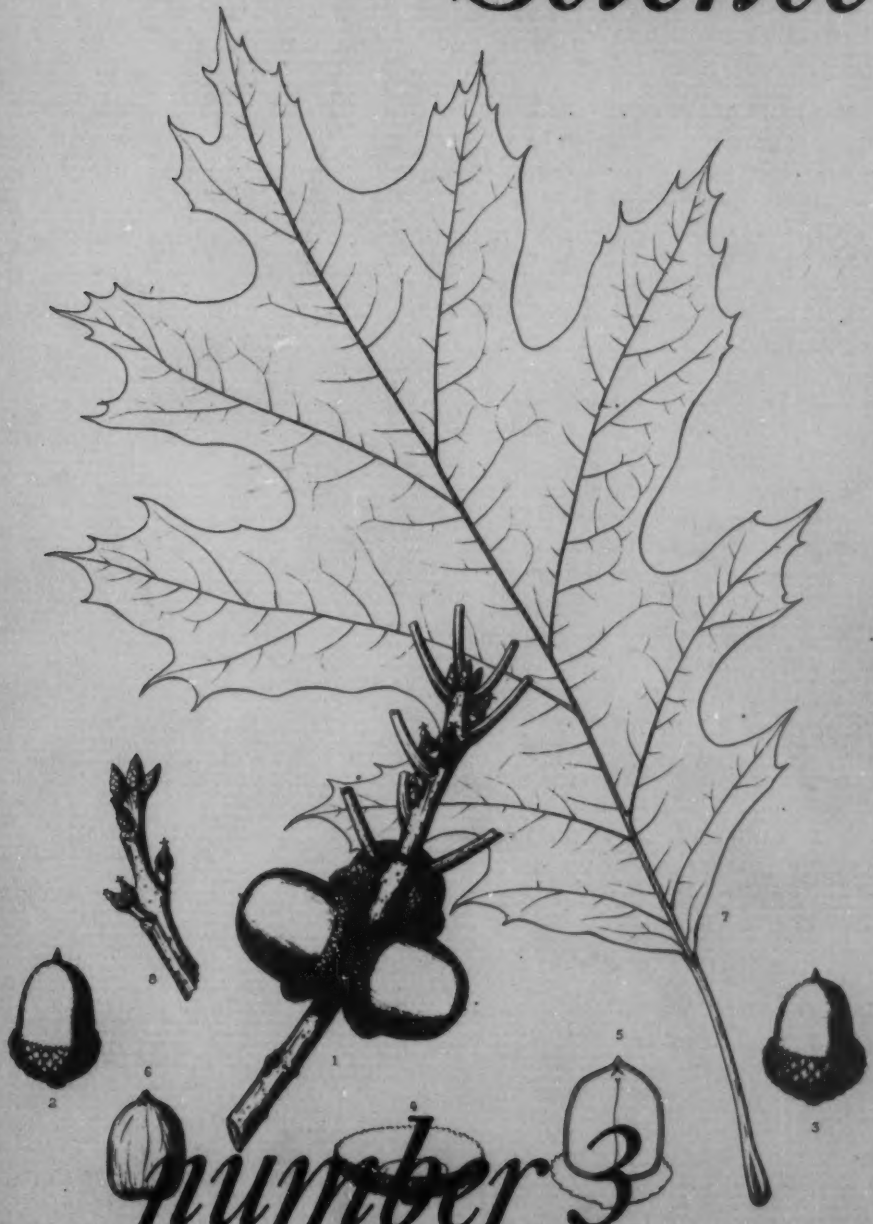

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Development of Compression Wood in Eastern White Pine Through the Use of Centrifugal Force

BY

DAVID R. M. SCOTT
STEPHEN B. PRESTON

COMPRESSION WOOD (redwood, rotholz) develops naturally on the lower side of any part of a coniferous tree that is inclined from the vertical plane. This abnormal formation apparently functions in strengthening any leaning stem and perhaps forcing it into an upright position.

Lumber containing compression wood frequently warps excessively and is unreliable in its mechanical properties, often being inferior to normal wood of the same weight in strength and elasticity along the grain. Thus, it is undesirable for many uses.

Compression wood is characterized by redness of color and a high proportion of summer wood. Anatomical abnormalities include changes in the tracheids, particularly in shape, wall thickness, and angles of fibrils in the secondary wall (Pillow and Luxford, 1937; Brown *et al.*, 1949). Important literature pertaining to the basic causes of compression-wood formation has recently been consolidated and summarized by Spurr and Hyvärinen (1954).

One concept, as indicated by the common English name, is that compressive force, or a differential in compression and tension, is the cause. Engler (1918) attributed eccentricities of growth on the upper side of leaning stems to geotropism, on the lower side to compressive forces. Jaccard (1919) found that if the stem of a conifer was bent alternately north and south, or rotated in a vertical plane, no compression wood was formed unless the stem remained in one position for a definite period of time. Later, the same investigator placed growing trees on a horizontal turntable and subjected them to centrifugal force (1939). The coniferous stems developed compression wood on the outer sides. Any new terminal growth tended to bend inward against the centrifugal force. Jaccard concluded that the tension-compression differentials developed by these conditions were the cause of compression wood formation.

Sonntag (1904) offered the theory that differences in light intensity between the top and bottom of leaning stems might lead to the development of compression wood.

Ewart and Mason-Jones (1906) refused to accept either compression or light theories, but rather felt that compression wood was caused by gravity. To support this conclusion it was shown that when

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growing stems were bent in complete vertical circles, compression wood formed on lower sides independent of whether the particular section was in tension or compression. Similarly, it was proved that shaded or lighted conditions of growth made little difference in compression wood formation.

White (1908) added to the findings of Ewart and Mason-Jones. Trees were placed on a vertically rotating table, where it was found that one rotation every four hours produced compression wood, although one every two minutes did not. Trees were also grown in a horizontal position, supported throughout their length to eliminate any compressive force. Even under these conditions compression wood was produced on the lower sides. Leaning stems were covered with tinfoil to eliminate light differences, a treatment which did not prevent normal compression wood development.

On the basis of this past evidence, it could be concluded that gravity and compression wood formation are closely related. It was to further test this relationship that the present experiment was undertaken.

Method

In order to examine the effects of gravity more completely, it seemed necessary to develop compression wood under controlled conditions simulating gravity, but independent of it. This objective suggested the use of centrifugal force. Apparatus similar to that of Jaccard (1939) was used but with one important modification: bending was eliminated.[1] Jaccard did not support the trees in a vertical position and, as a result, centrifugal force undoubtedly caused them to bend outward, away from the vertical, at least until compensating compression wood formed. This bending would bring gravity and bending stress into effect as on any leaning stem, and would confound these effects with those of the centrifuging.

As shown in Fig. 1, each stem in this experiment was supported by a metal rod that was strong enough to resist the centrifugal forces used. Large, relatively straight, 4-year-old (2-2) white pine (*Pinus strobus* L.) trees were planted in individual pots. The pots were securely bracketed to the turntable and the stems of the trees were bound to the vertical rods at several points with grafting rubbers. The vertical position of trees and rods was checked with a level.

The turntable was driven by a 1/5 h.p. electric motor, and rotated at a speed to produce a centrifugal force approximating gravity.

Centrifuging was started on May 25, 1953, and continued until January 6, 1955, with a few breaks, rarely lasting more than several hours, for repairs or servicing. The trees were watered regularly throughout this period, but were otherwise untended except to renew the grafting rubbers on two occasions.

On January 6, 1955, the trees, after being marked to show orientation on the turntable, were removed from the pots. Each internode was cut off and the cut surfaces were examined with a hand lens. Two

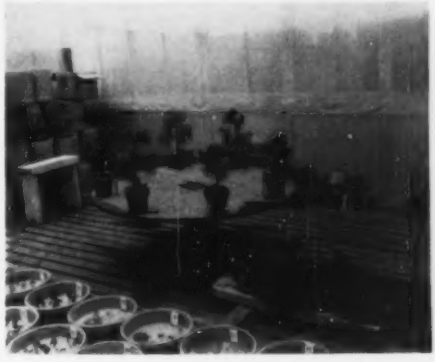

FIGURE 1. Apparatus used in experiment showing turntable, motor, and pots.

[1]Harold J. Lutz, Professor of Silviculture, School of Forestry, Yale University, first suggested this approach to the senior author in 1948.

typical trees were selected for detailed examination. Transverse microtome sections were prepared from each of the three internodes of the two trees and were examined carefully for anatomical evidence of compression wood formation. Thus, sections from two supported and one unsupported internodes of each tree were studied. Permanent, stained mounts were prepared only for sufficient sections for photographic illustrative purposes.

Results and Discussion

It was apparent before the trees had been removed from the turntable that compression wood had formed, or at least had influenced the terminal growth, during the period of treatment. As Jaccard had previously shown, this growth tended to lean sharply toward the center of the table (see Fig. 2). Although difficult to measure accurately, the angle of this deviation approximated 25° to 30° from the vertical. This is 5° to 10° more than indicated by Jaccard, but it should be remembered that in his experiment, centrifugal forces of about 40 percent of gravity were used as compared to 100 percent in the present investigation. It is probably safe to suppose that this leaning position is essentially the same as an upright position under normal growing conditions. That is, the 25° to 30° lean inward balanced the centrifugal force, although it might be theorized that a 45° angle would approximate an upright position under normal conditions of growth. The duration of the experiment allowed only one year's growth to assume this angle. It would be interesting to duplicate the conditions for several growing seasons to find if the angle remained constant. In addition, concurrent tests using several centrifugal forces in order to determine the different angles from the vertical assumed by the trees should be revealing.

FIGURE 2. Close-up, illustrating the method of holding the trees upright, and the inward lean of new terminal growth.

The hand lens examination revealed pronounced compression wood on the outer side of the vertically supported portion of the stem (Fig. 3). The growth was exceedingly eccentric with the pith being furthest from the side of the seedling oriented outward from the centrifuge. The abnormal growth appeared to be largely latewood, reddish in color, and lusterless, whereas the growth closest to the hub of the centrifuge appeared nearly normal.

The abnormal growth of the outer side of the supported stem displayed all anatomical characteristics of compression wood (Fig. 4). The tracheids were more or less round in cross section and abnormally thick-walled, and the secondary walls contained many spiral shrinkage checks. Numerous interstitial spaces were present. The tissue formed on the side of the tree closest to the hub appeared normal in every respect.

Of significance is the fact that the unsupported portion of the stem which was inclined toward the hub exhibited neither gross nor anatomical characteristics of compression wood. This supports the previous supposition that the leaning position for these seedlings of 25° to 30° from the vertical approximates the upright position under normal conditions with respect to reaction growth. Obviously, as previously noted, there is an outward component of force normal to the longitudinal axis of the inclined portion of the stem which, in this

case, would amount to approximately 90 percent of gravity. The true gravity component normal to the stem and opposite the centrifugal component is approximately 42 percent of gravity. This condition suggests a possible stress-gravity relationship which bears investigation.

It can be concluded that centrifugal force alone was responsible for the development of compression wood in the vertical portion of the stems. The evidence is too uniform to allow any other conclusion. It would seem reasonable to carry this reasoning forward and conclude that gravity

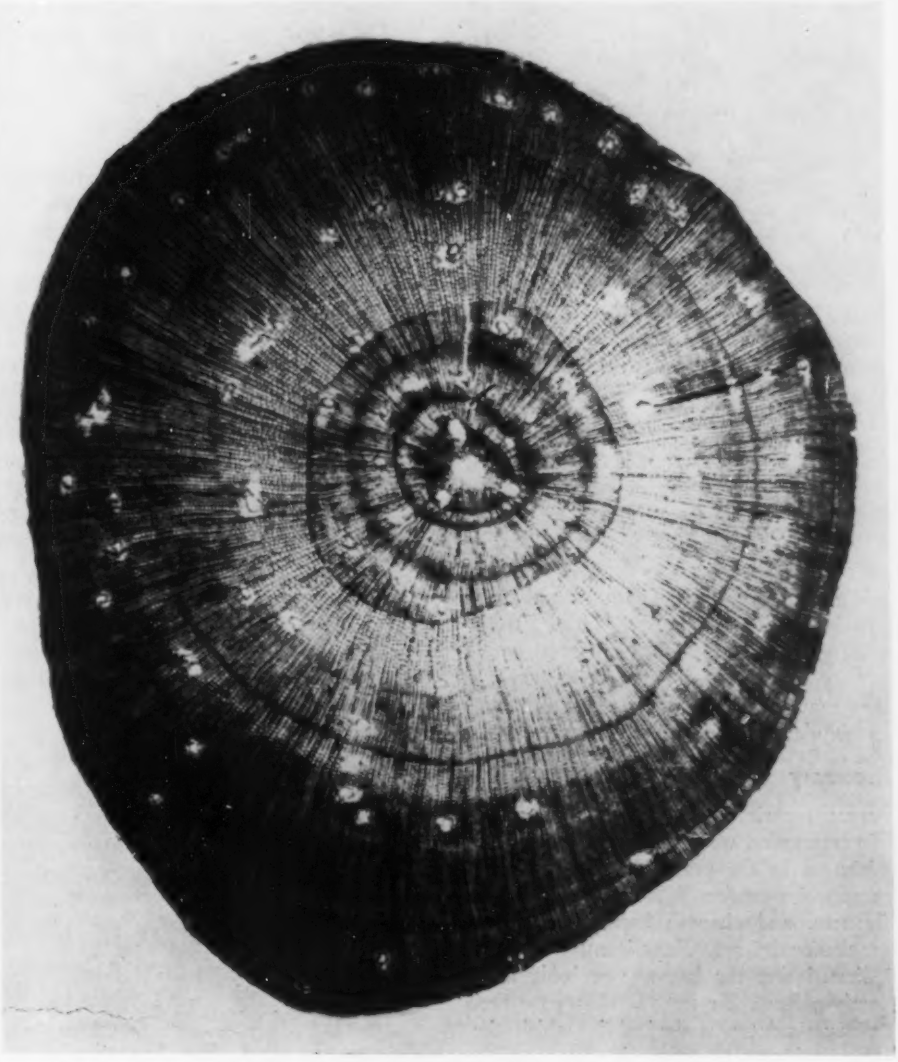

FIGURE 3. Cross section of supported portion of stem (12.5×) showing eccentric growth and abnormal latewood formation.

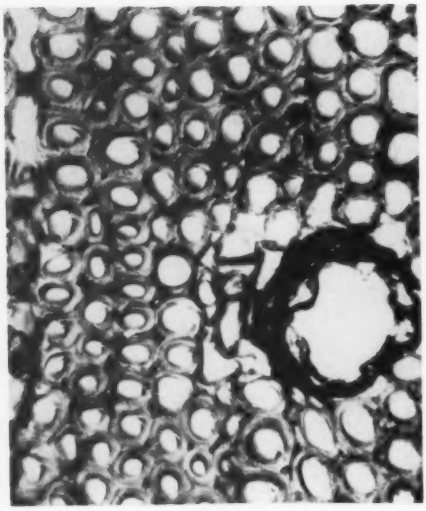

FIGURE 4. Cross section of outer part of supported stem (150×) showing pronounced compression wood. Note circular, thick-walled tracheids and numerous interstitial spaces.

might have the same effect on leaning stems. If the evidence in this experiment is added to that of Ewart and Mason-Jones (1906) and White (1908), it must be conceded that gravity is a factor which may be solely responsible for the formation of compression wood in nature. Until further evidence is available with respect to stress-gravity interactions, it is unsafe to conclude that gravity is the only factor which may so stimulate compression wood growth.

Summary

Several theories concerning the basic causes of compression wood formation have been advanced in the past. Among these are compression-tension differences, light differences, and changes brought about by gravitational force. Experimental evidence indicated that the last was probably most nearly correct. To test this theory further, an experiment was devised in which the effects of gravity were simulated under controlled conditions by subjecting vertically supported stems to centrifugal forces approximating gravity. The resulting development of compression wood gives further evidence that gravity is a cause of compression wood in nature.

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Survival Value of Dew Under Laboratory Condition with Pinus Ponderosa.

BY
EDWARD C. STONE
HARRY A. FOWELLS

THE CONCEPT that dew is an important micro-environmental factor is not a new one. As early as 1727 it was demonstrated that water could move inward through leaf surface as well as outward (Hales, 1727). Subsequently, a long procession of researchers have presented data pertaining, at least in part, to the problem of dew and its utilization by the plant. In general they agree that plants are capable of absorbing water through their leaf surfaces but they do not agree upon its effectiveness (Krecmer, 1951; Stephan, 1942).

Specific research dealing with dew and forest trees is not as voluminous. Some of the more interesting field studies, however, have been conducted with this type of plant material. (Arvidson, 1951; Eisenzopf, 1952; Firbas, 1931; Gates, 1914; Hiltner, 1930, 1932; Leick, 1933; Michaelis, 1934a, 1934b; Rouschal, 1938; Stalfelt, 1944).

Gates (1914) used cut branches of black spruce and several evergreen shrubs in Michigan and found that moisture gained from the atmosphere on frosty nights or nights of high humidity was equal to three or four times the amount lost by transpiration on a cold winter day.

Twenty years later Michaelis (1934a, 1934b), in a more elaborate investigation carried on in the Swiss Alps, came to the same conclusion. He followed the water balance in spruce branches that were cut off in December and suspended until March under the shade of the crowns. The loss in weight of these branches was less than would be expected from transpiration measurements. Therefore, he assumed that part of the transpirational loss was replenished by the dew that formed at night.

Stalfelt (1944) also worked with spruce in southern Switzerland. He found that, under drought conditions, water absorption through the needles amounted to as much as thirty percent of the transpirational loss. He concluded, therefore, that water absorption by the needles was a very significant ecological factor. In this particular area, he decided that most of the water thus absorbed came from rain and that dew furnished only a minor amount.

Arvidson (1951) carried out field measurements on the Isle of Oland in southeastern Sweden where summer drought conditions often develop. Here many shrubs and trees, such as ash, oak, and poplar utilized atmospheric moisture by absorbing it through the leaves. Rain, dew and fog all appeared to be important sources of moisture. He reported that in late summer the

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Work carried on under University of California Agricultural Experiment Station Research Project 1577 in the Forest Physiology Laboratory. Stone is Assistant Professor, School of Forestry, University of California, Berkeley. Fowells is with the Division of Forest Management Research, Forest Service, U. S. Dept. of Agric., Washington. He was formerly Silviculturist, California Forest and Range Experiment Station, U. S. Dept. Agric., Berkeley.

nocturnal uptake of dew may exceed the daily transpiration loss even in the absence of soil drought.

Recent reports by Breazeale *et al.* (1950, 1951), and Breazeale and McGeorge (1953a, 1953b) have created renewed interest in the *modus operandi* of dew. Their greenhouse data indicate a reverse movement of water through the leaves, down the stem and out into the soil when the tops of tomato plants are exposed to a continuous spray. Already several papers by other investigators, both in opposition and in support of this concept have appeared (Haines, 1952, 1953; Hohn, 1954; Janes, 1954), and more are undoubtedly on the way.

The study presented below was initiated as a consequence of two earlier reports concerned with the drought resistance of pine. The first one, by Fowells and Kirk (1945), showed that ponderosa pine could survive in soils after moisture had been gradually reduced to the permanent wilting point as determined with sunflowers. The second one, by Stone, Went and Young (1950) demonstrated that Coulter pine in soil gradually reduced to the permanent wilting point could remove water vapor from the surrounding air once the relative humidity reached ninety percent or higher.

These data when viewed together suggested that high humidities as well as dew might play an important role in seedling survival.

To test such a possibility requires several steps. The experiment described below is the first step; namely, to determine whether or not artificial dew is capable of increasing the survival of pine seedlings when the moisture content of the soil surrounding its roots has been gradually reduced to the permanent wilting point.

Method of Study

In March, two-year-old ponderosa pine seedlings, with roots trimmed to about four inches, were planted in gallon cans of Oakley sandy loam. The moisture equivalent of this soil was 3.5 percent, and the permanent wilting point 2.4 percent as determined with sunflowers. One seedling was planted in each of 50 cans. By September their root systems were well-developed throughout the lower two-thirds of the can.

At this time, forty cans were selected for the experiment on the basis of the uniformity of the seedlings. Five sunflower seeds were then planted around each pine seedling. After germination the sunflowers were thinned to three per can and allowed to develop. Because of the low fertility of the soil an occasional watering with IN Hoagland's solution was required for good sunflower growth.

When all the sunflowers had developed at least twelve fully expanded leaves, watering was discontinued for the remainder of the experiment. The roots of the sunflowers had completely permeated the soil mass in the cans at this stage of development (Fig. 1).

After watering was discontinued, the moisture content of the entire soil mass was first reduced to the permanent wilting point (when the sunflowers permanently wilted) and then to the ultimate wilting point (when they died) (Furr, 1945; Taylor *et al.*, 1934).

Nine days after watering was discontinued, all of the sunflowers but none of the pines were dead. Soil moisture content was then determined in ten of the cans. In the thirty cans left, the dead sunflowers were clipped off at the ground level and each can was sealed with a plastic envelope through which the pine seedling protruded. A water-tight seal around the stem was effected with several turns of a fine copper wire and a heavy wrapping of electrical scotch tape. The bottom edge of the plastic envelope was sealed to the can with more electrical scotch tape. Drain holes in the cans were sealed with hot paraffin (Fig. 2).

These thirty cans were then placed together on the same bench in the greenhouse. During the day all cans were kept together. For twelve hours every night, however, fifteen of the sealed cans were placed under a mist spray to simulate dew.

FIGURE 1. Can cut away to show distribution of roots. The dark roots shown behind the white piece of paper are pine roots. The light-colored roots belong to the sunflower plants.

FIGURE 2. Can covered with plastic envelope after the sunflowers had died and had been clipped off.

The fifteen cans which were not moved were exposed only to the normal greenhouse humidity which ranged from twenty to eighty percent.

The weight of each can was taken periodically, principally as a check for leaks under the spray. Leaks were found in only two of the cans with seedlings receiving spray. The leaks were indicated by a gain in weight and confirmed by the presence of wet spots.

As the pine seedlings died, the dates were recorded and the soil moisture content was determined for each inch of depth within each can. Three samples were taken from each inch layer of soil as it was dug from the can, and the moisture content per layer was expressed as the average of the three.

Five cans from each group were used during the experiments as a check on the reliability of the death-point estimate. From time to time a plant considered either dead or alive was removed and water added. In every case where the plant was assumed dead, water did not revive it; and conversely, in every case where the plant was considered alive, it continued to grow after water was added. For a two or three-day period one could not be sure whether the plant was alive or dead. This short time, however, probably did not materially affect the results.

Results

All the pine seedlings continued to live for some time after the sunflowers died. The average number of days to death, from the time the last sunflower had died, was 21 for the group of pine seedlings which did not receive spray at night and 41 for the group which, in contrast, did receive spray at night. The range of the data was 18-29

days and 37-45 days, respectively, for the two groups of plants. The difference between the mean values obviously is significant.

It thus appears that two separate, although perhaps closely related, phenomena are operating. The first is the ability of the pine seedling to survive after the soil moisture is reduced to the ultimate wilting point (death point) of the sunflower. And the second is the ability of the pine seedling to survive even longer at such low soil moisture levels if dew (spray in this experiment) occurs at night.

Both groups of pine seedlings continued to remove moisture from the soil even after the ultimate wilting point of the sunflower had been reached. Except in the top two inches, the soil moisture content throughout the cans containing pine seedlings, regardless of whether they received spray at night or not, was significantly lower than in other cans containing only sunflowers (Table 1). Statistical significance was established by variance analysis of the data of the three groups of test plants.

When the pine seedlings died, the moisture content of the soil surrounding their roots was dependent upon whether or not the seedlings had received spray at night. If they had not, the soil moisture content was in general significantly lower than if they had.

The root distribution of the pine seedlings shown in Table 1 explains the absence of any significant relationship between treatment and moisture content in the upper two inches of soil. Since there was only an occasional small pine root in this zone, the low moisture content was due primarily to water removal both by sunflower roots that permeated the zone and direct evaporation from the soil during the interval between the cessation of watering and the death of the sunflowers.

TABLE 1. Distribution by depth of soil of the roots of pine seedlings and the soil moisture content at death of seedlings, sprayed and not sprayed, and of sunflowers.

Depth	Distribution root system	Soil Moisture Content: Pine seedlings not sprayed at night	Pine seedlings sprayed at night	Sunflower ultimate wilting point
Inches		*Percent*		
0-1	0	0.7	0.7	0.7
1-2	trace	0.8	0.8	0.9
2-3	5	0.8	0.9	1.3
3-4	10	0.8	1.1	1.5
4-5	25	0.9	1.0	1.5
5-6	60	0.9	1.1	1.5

Discussion

In brief, these data are important because, first, they substantiate earlier work that indicated pine seedlings are considerably more resistant to permanent wilting than sunflowers (Fowells and Kirk, 1945; Stone *et. al.*, 1950). Second, they indicate that dew can prolong the life of pine seedlings subject to high soil moisture stress.

The structure of the pine seedling is an obvious reason why it is more resistant to permanent wilting than the sunflower. The needles, the twig, and the main stem of the pine seedlings all become shrunken as the moisture stress increases; but they do not collapse, and with added moisture become turgid again. In contrast, the leaves of the sunflower collapse under high moisture stress. Iljin (1953) found that other factors affect the relative ability of different plants to survive desiccation. Relative cell size, vacuole size, osmotic concentration of the cell sap are all important.

Theoretically, the amount of water lost from the soil after the death and subsequent removal of the sunflower is dependent both upon the vapor pressure gradient between the roots of the pine seedling and the air surrounding its exposed top, and upon the length of time the seedling remains alive under these conditions. Thus, a reduction in the soil moisture to its lowest value might therefore, be expected from a combination of circumstances which either prolongs the life of the seedling, increases the moisture stress within the plant, or both.

The data can be interpreted to support this expectation. The life span of the pine seedling was increased by dew (artificial in this case) which reduced the moisture stress within the plant and the vapor pressure gradient between the plant and the surrounding air. The combined effect apparently still allowed some reduction in soil moisture, but not as much as when dew was withheld. When dew was withheld, the moisture stress in the seedling was greater, although the period of time the plant remained alive was shorter.

This interpretation of the data does not agree with that of Breazeale et al. (1950, 1951, 1953a, 1953b). They concluded that there is a backward movement of water through the plant and out of the roots into the soil, at least when the top is exposed to a continuous spray. Certainly no such interpretation can be applied to the data presented in Table 1.

The specific role of dew in increasing survival under the conditions of the above experiment is still undetermined, although a reduction in the moisture stress is assumed. This would be accomplished by a complete or partial resaturation of the needle tissue each night. Whether or not any of this moisture moves down into the roots is still a point of conjecture.

Throughout this paper, dew has been considered as synonymous with the mist spray treatment. Obviously, the two are different but it is assumed that once the plant is covered with drops and later a thin film of liquid water, the reaction of the plant is essentially the same. High relative humidities at night would be expected to produce effects similar to dew except for the magnitude. The exact difference must be determined experimentally.

Conclusions

Under greenhouse conditions artificial dew at night increased the survival of ponderosa pine seedlings subject to high soil moisture stress.

The data suggest the possibility that the regular occurrence of dew at night could be of survival value to ponderosa pine seedlings growing on soils that generally reach the wilting point by late summer or early fall. However, field tests will be required to determine where and when the presence or absence of dew at night becomes an important factor in survival.

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Corrigendum

In *Chlorisis, mycorrhizae and the growth of pines on a high-lime soil* by Jim Dale, A. L. McComb, and W. E. Loomis (FOREST SCIENCE 1: 148-157), two errors occurred in the figure captions. In Fig. 1, the pH of the surface soil should be 7.8 instead of 7.1. In Fig. 2, the chemical formula should be $Fe_2(SO_4)_3 \times H_2O$. *Ed.*

The Primary Leaf as an Indicator of Physiologic Condition in Shortleaf Pine

BY

F. H. BORMANN

THERE ARE TWO TYPES of shoots in pine: dwarf (spur) shoots which bear secondary leaves, usually arranged in fascicles; and long shoots which bear primary leaves in whose axils dwarf shoots arise (Coulter and Chamberlain, 1910). The form of the primary leaf varies with the developmental stage of the plant; in the young seedling it is needle-like, while in older plants it is reduced to a brown scale (Thomson, 1914).

The transition from needle-like to scale-like primary leaves in *Pinus echinata* Mill. usually occurs at the beginning or early in the second season. After this time, the long shoot has scale-like primaries. Numerous instances have been noted, however, in which trees of various ages produce primaries showing a reversion toward the needle-like type. This is especially true for young trees that have been topped; here basal sprouts develop with primary leaves bearing a great resemblance to the needle-like primaries of the first-year seedling.

Important questions arise in regard to these reversions: are they merely slight changes in gross morphology with little or no physiological implication, or do they carry with them deep-seated changes with the reverted shoot tending to assume the same physiology and anatomy as the first year seedling? In other words, the gross morphology of the primary leaf might serve as an indicator of the internal condition of the shoot.

As a preliminary test of this hypothesis, an attempt was made to root cuttings from stump sprouts bearing needle-like primary leaves. Since it has been shown by numerous experiments that cuttings taken from one-year-old pine trees (which bear needle-like primaries, Thomson, 1914) root readily (Thimann and Behnke-Rogers, 1950), and that the capacity to root decreases rapidly with age (Thimann and Delisle, 1939; Mirov, 1944), sufficient rooting by these cuttings might be taken as evidence of a return to the first-year condition.

Method

On the mornings of July 21 and 22, 1954, two sets of 100 greenwood cuttings were collected from stump sprouts, 6 to 12 inches in length, of small detopped trees growing in a relatively open field on the Emory University campus. The age of these trees, which were occasionally topped by mowing, was estimated to be three to four years on the basis of an examination of the annual rings in the uppermost portion of the root.

The sets of cuttings, from trees of approximately the same age, were in slightly different developmental stages. The first set contained small succulent cuttings on which the secondary needles had not yet developed, and, consequently, the needle-like

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primaries formed 100 percent of the foliage (this set of cuttings is hereafter called PN). The second set was composed of slightly harder cuttings in which developing secondary needles formed about 50 percent of the foliage, while needle-like primaries formed the remaining 50 percent (these cuttings are hereafter called PNS).

The basic experimental design was a block of two pairs of 4-inch clay pots filled with sand, each pot of one pair containing five cuttings of the same developmental stage. The cuttings of one pot of each pair were treated with Hormodin number 2, 0.3 percent indole-butyric acid (IBA), while the remaining pot was the untreated control.

The basic design was replicated ten times on a bench in a moderately sunny room of the Emory University greenhouse. The whole experiment was then enclosed in a three-layered cheesecloth cover supported about 18 inches above the cuttings by a wooden frame to reduce light and to improve humidity conditions. Later, as the natural light decreased, layers of the cover were progressively removed until during the autumn the cuttings were entirely uncovered.

The cuttings were watered once or twice a day. Occasionally notes were made on the condition of the cuttings in each treatment. No record was made of temperature; however, the days during July, August, and September were exceptionally warm, the summer of 1954 being one of the hottest on record.

The author is indebted to Mr. Deems Wiggs of the Biology Department of Emory University for his help in setting up and caring for the experimental plants.

Results

On lifting the cuttings on January 16, 1955, it was found that excellent root formation had occurred in both developmental stages. In practically all instances where roots formed they resembled those of first-year seedlings with a well developed tap root and with several strong branches (Fig. 1). Although a greater number of PN than PNS cuttings rooted, the difference was not statistically significant (Tables 1 and 2). In callus formation, how-

TABLE 1. Callus and root formation.

Developmental Stage	Treatment	Callus formation		Root formation	
		Number	Percent	Number	Percent
PN	Hormodin No. 2	8	16	3	6
	Control	44	88	16	32
PNS	Hormodin No. 2	1	2	0	0
	Control	24	48	10	20

TABLE 2. Statistical analyses.

Source	DF	Callus Formation		Foot Formation	
		MS	F	MS	F
Treatment	1	87.023	89.4**	13.225	22.6**
Development Stage	1	18.225	18.7**	2.025	3.5
Block	9	1.225	1.3	0.525	0.9
T-DS Interaction	1	4.225	4.3*	0.225	0.4
Error	27	0.973		0.584	
Total	39				

*Significant at 5 percent level.
**Significant at 1 percent level.

ever, the stage of development apparently was important since cuttings with developing secondary needles (PNS) had a significantly lower amount. Results of Hormodin treatment, 0.3 percent IBA, were highly significant in depressing root and callus formation in both developmental stages. In callus formation, the treatment-developmental stage interaction was significant at the 5 percent level (Table 2), probably due to the severe anticallusing effect of Hormodin on cuttings of the PNS stage. These auxin effects were not entirely unexpected since periodic observation indicated that a number of treated cuttings were dead or dying.

It should be noted that up to the present time, July, 1955, practically all of the rooted cuttings show a marked degree of chlorosis.

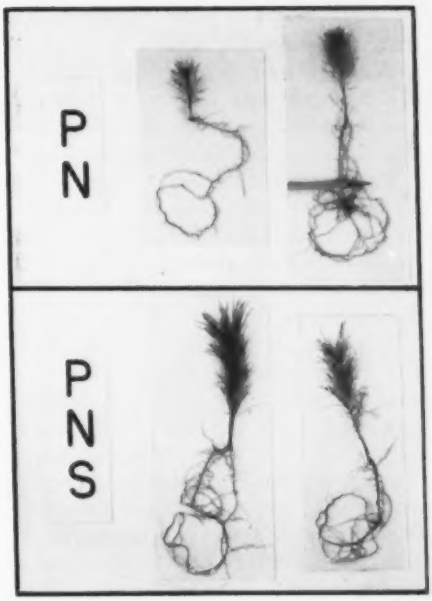

FIGURE 1. Rooted cuttings from plants on which secondary needles had not yet developed (PN) and from plants with about half secondary needles (PNS)

Discussion

Cuttings of older plants exhibiting a gross morphology similar to first-year seedlings have a definite ability to root. The fact that cuttings with a slightly advanced stage of development (PNS) show far less callus formation than less advanced cuttings (PN) might indicate that a developing sprout soon loses its ability to callus and, perhaps, to root.

The negative effect of auxin on callus and root formation on these cuttings with needle-like primaries is in contrast to the many positive auxin effects reported for pine cuttings on which the primary leaves were probably represented by scales. Although this negative effect may have been due to an improper auxin level, it might also be indicative of a fundamental difference between seedling and reverted twigs with needle-like primaries and normal twigs of older plants with scale-like primaries. In this regard, it may be noted that Thimann and Delisle (1939) have reported a negative auxin effect on cuttings from six-month seedlings of *Acer plantanoides* and *Pinus strobus*.

The basic question as to whether these sprouts with a gross morphology similar to first-year seedlings show a greater ability to root than normal 3- to 4-year-old seedlings is difficult to answer. Since Mirov (1944) obtained 50 percent rooting with cuttings from normal 3-year-old shortleaf pine (probably with scale-like primaries), it would appear that the ability of sprout-cuttings, in the present study, to root is not greatly different from the normal for this age. On the other hand, Zak,[1] after many trials, was unable to root any cuttings from 5-year-old shortleaf, and more recently, Zak[2] was able to obtain only 4-16 percent rootings with cuttings from 3- to 4-year-

[1]Zak, B. 1948. Vegetative propagation of shortleaf pine. U. S. For. Serv. Stheast. For. Exp. Sta. unpub. rep.

[2]Zak, B. 1953. The rooting of shortleaf pine cuttings. U. S. For. Serv. Stheast. For. Exp. Sta. unpub, rep.

old trees, and 4-8 percent with material from a 35-year-old plant.

Although these data are not conclusive, it is significant that 32 percent of the PN controls rooted, and 88 percent callused, despite the fact that the cuttings were taken at the height of the summer, a season little conducive to rooting,[3] and were maintained for several months under far-from-ideal conditions in the greenhouse. This may be indicative of a greater rooting potential than shown by the data.

It is apparent that further work along these lines is required. Attempts should be made to evaluate the rooting response of PN cuttings from stump and crown sprouts of older shortleaf pines. The latter type sprouts have been noted to occur in profusion after the lower 1/2-2/3 of the crown of young trees, up to approximately 20 years of age, has been burned off by severe ground fires.

[3]Dorman, K. W. 1947. Summary of propagation experiments from the vegetative propagation of naval stores pines. U. S. For. Serv. Stheast, For. Exp. Sta. Third Progress Report (Unpublished).

This information should not only have a bearing on the practical problem of rooting, but also on the important theoretical probems dealing with the factors regulating growth and development of pine.

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Effect of Interrupted Dark Period on Height Growth of Two Tree Species

BY
ROBERT ZAHNER

NUMEROUS PLANT RESPONSES are influenced by the relative length of day and night. Most familiar are the effects of photoperiodism on flowering and fruiting of crop plants. Less obvious, but nevertheless active, is the influence of the dark period on the growth of forest trees.

Photoperiod has been shown by the early work of Garner and Allard (1923) to be an important factor in the periodicity of growth in woody species. More recently, Kramer (1936) reported that certain tree species, among them yellowpoplar (*Liriodendron tulipifera* L.) and loblolly pine (*Pinus taeda* L.), made considerably less growth and became dormant sooner under short-day photoperiod than under normal-day conditions. Under photoperiods of long day or continuous day, Kramer found these two species grew well all year round.

Wareing (1950) found Scotch pine (*Pinus silvestris* L.) made better growth when subjected to an interrupted dark period than when grown with normal dark period. Following Wareing's lead, the present investigation concerns the regulatory effects of interrupted dark period during short-day treatment on the height growth of loblolly pine and yellowpoplar.

The Experiment

Twenty-four one-year-old loblolly pine seedlings were divided randomly into two groups of twelve each. An equal number of yellowpoplar seedlings were similarly grouped. Individual trees were planted in 8-inch pots on March 1, 1952, and the height of each recorded. One group of each species, hereinafter termed the control group, was subjected to a treatment of 9.5 hours of light alternating with 14.5 hours of darkness. The other group of each species was given the same treatment except that the dark period was interrupted in the middle by a half-hour period of artificial light. The 9.5-hour light period was between the hours of 7:45 a.m. and 5:15 p.m., and was by natural sunlight alone; the half-hour interrupting light period was provided by two standard 200-watt white lamps suspended about 3 feet over the plants. All groups of plants were kept under similar greenhouse conditions of temperature and supplied with ample soil moisture.

The heights of seedlings were measured twice monthly from March 1 through October 1, 1952. Average increments in height of the twelve individuals in each group were calculated for the semi-monthly intervals. Plots of growth increments were made versus time for each group as shown in figure 1.

Based upon graduate work under Dr. Paul J. Kramer at Duke University. The author is now at the Crossett Experimental Forest, Forest Service, U. S. Dept. Agric.

Results

The rate of height growth for those trees subjected to the interrupted dark period treatment was greater throughout the study than the rate for those trees under control treatment. The effect of the interrupted dark period appeared early in both species: after four weeks for the yellowpoplar, and after only two weeks for the pine. The loblolly pine under the control conditions almost ceased growth early in May, while the yellowpoplar under this treatment ceased in early June. Growth of both species under the interrupted dark period treatment, however, continued into September, with a final result for the growing season of more than twice the total growth in height of the control trees.

Discussion

Height growth of both species was affected similarly and to the same proportion by the interrupted dark period. The brief light period after 7 hours of darkness was evidently responsible for increased height growth. The photoperiod resulting from this treatment was one of two short dark periods in a 24-hour cycle. The control treatment consisted of short day and long dark periods in the same cycle. Thus the net effect of the comparison was perhaps growth under long dark period versus growth under short dark period.

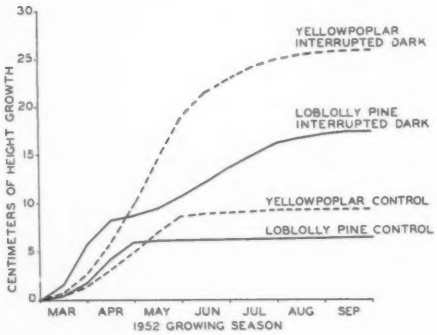

FIGURE 1. Plots of growth increments of loblolly pine and yellowpoplar grown with (1) a 9.5-hour photoperiod and uninterrupted dark period (control), and (2) the same photoperiod but with the dark period interrupted in the middle by a 30-minute light period. Height growth is plotted as the average value of (L_t-L_o), where L_o is initial height and L_t is height at any given time thereafter.

Photoperiodic responses of yellowpoplar and loblolly pine can be explained by a theory presented by Wareing (1950, 1951). In the mechanism of photoperiodism, he assumes the formation of a growth inhibitor during the dark period. The inhibiting substance is unstable after dark periods of short duration, and is destroyed by light. Long periods of darkness result in a stable inhibitor.

In the present study, an inhibitor-system could have become operative during the long dark period of the control treatment. Growth ceased early. The interrupted dark period treatment, however, did not afford an immediate buildup of the stable inhibitor. Growth continued in proportion to the length of the dark period. At the extreme, as under continuous-day treatment (Kramer, 1936), growth could theoretically continue indefinitely, for no inhibitor would be formed.

Kramer (1943), reported correlations between height growth and photoperiod for these same two species under normal day conditions. Dormancy was broken in the spring when nights became short, and growth continued until fall when the dark period again lengthened. Under these normal conditions, loblolly pine seedlings made considerably more total growth than did yellowpoplar during the same season. The reverse was found to be the case in both treatments of this study. It may be that yellowpoplar is less sensitive to the effects of the dark period than is loblolly pine.

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Die Bedeutung der Fadenpilze als Symbionten der Pflanzen für die Waldkultur (The importance of filamentous fungi as symbionts of plants for silviculture.) By Richard and Marianne Falck. 1954. J. D. Sauerlander, Publisher. Frankfurt am Main. 92 pp.

REVIEW by Th. Keller

Department of Soils, The University of Wisconsin

THIS BOOK is a summary of lifelong research in mycotrophy, initiated in the beginning of this century and continued with certain interruptions to the present day. In the last phases of investigations Dr. R. Falck was assisted by his daughter Marianne who worked at the Oglethorpe University in Georgia (U.S.A.).

The introductory part of this publication presents a well illustrated outline of the different forms of mycotrophy, encountered in herbs (orchids, Ericaceae) and trees. The following chapters deal with the decomposition of litter and other lignified matter by *Basidiomycetes*. The distinction is made between "corrosion" and "destruction." Decomposition processes in which cellulose and lignin are destroyed simultaneously are called corrosion. In destruction only cellulose is attacked, leaving a lignin-enriched residue which promotes the formation of an acid layer of inert raw humus. In the opinion of the writers, the myrcorrhiza-forming *Basidiomycetes* contribute to the decomposition of lignin and thus maintain a highly productive humus type. As a result of observations in pine forests of Europe and the State of Georgia the authors believe that mycorrhizal fungi exert favorable nutritional effects and also protect their higher symbionts from parasitic fungi.

The pamphlet contains a review of the senior author's ideas on plant feeding, which were first published in 1923. This is prefaced with a history of the subject since von Thaer and Liebig. His theory stresses the importance of mycorrhizal fungi not only in the mineral- and nitrogen-nutrition but in the carbohydrate metabolism as well. This "organic feeding" in which the host plant is provided with carbyhydrates from the soil humus is supposed to support or partially replace the photosynthetic process. It is believed to be of special importance on poor and dry sites because the absorption of carbohydrates reduces the water necessary for the formation of sugar and other organic compounds. This point of view stresses therefore the importance of highly productive humus forms.

For all those who are interested in mycorrhizal problems the information of this book might be valuable.

The Taxonomy and Evolution of the Sawfly Genus Neodiprion

BY
HERBERT H. ROSS

LARVAE of the genus *Neodiprion,* one of several genera belonging to the sawfly family *Diprionidae,* feed exclusively on the plant family Pinaceae, especially the genera *Pinus, Picea, Tsuga* and *Abies.* With the exception of a single Palearctic species, members of the genus occur only in North America. Many species of *Neodiprion* cause extensive defoliation of valuable timber species of the Pinaceae, so that a thorough knowledge of the genus is of great importance to the forester.

In 1943 Atwood and Peck published an outstanding diagnostic work on this genus, treating in detail 12 species found in eastern Canada on various species of pine. Efforts to correlate the excellent concepts given by Atwood and Peck for the Canadian species with the species units occurring to the south and west proved difficult because it appeared, first, that apparently identical larval colonies produced adults which were demonstrably different and, second, demonstrably different larvae produced adults which appeared virtually identical. Repeated rearings of *Neodiprion* colonies by forest entomologists finally resolved a considerable number of these questions beyond reasonable doubt.

Judging from these rearings, several species of *Neodiprion* are distinct biological and genetic units, yet can be diagnosed at present only on the basis of differences in larval color pattern or details of life history. In the case of certain other forms, it is difficult to ascertain whether the units involved are species or merely races of the same species.

The Western species of the genus are not well known. About a dozen distinct forms are diagnosed here, but it is entirely possible that these represent only a fragmentary portion of the total fauna.

This report is essentially a review of the status of *Neodiprion* for the entire continent. It is evident that we need more information and study in many areas, but it is hoped that this outline will integrate data on new taxonomic discoveries, geographic distribution, and host preference. A phylogenetic analysis of the genus offers several interesting suggestions concerning the past evolution and distribution of conifers and Diprionidae on the North American continent.

This study has re-emphasized the necessity for combining characters from all stages of the life cycle whenever possible in taxonomic studies. It further re-emphasizes the fact that taxonomic results are not always as clear-cut and practical from the standpoint of identification as we would like them to be.

Many persons and institutions have given material assistance to this study. Various laboratories of the U. S. Forest

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The author is head of the Section of Faunistic Suveys and Insect Identification, Illinois Natural History Survey, Urbana.

Service, Division of Forest Insect Research, the U. S. National Museum, the U. S. Entomological Research Branch, the Canadian Division of Forest Biology, the Canadian Division of Entomology, the University of Toronto, and the University of Wisconsin have been foremost among the contributors.

Key to Species[1]

1. Mesoscutellum with large, conspicuous punctures, especially on the lateral areas, or head and thorax entirely red combined with mostly blue-black abdomen ***Lecontei Group***—2

   Mesoscutellum with only fine punctures, restricted to the lateral areas, or without evident punctures; if abdomen is mostly black or blue-black, the head and thorax are also mostly dark ***Sertifer Group***—19

2(1). Saw with annuli 3 and 4 very divergent, as in figs. 5-8. Sheath with lateral margins high, often with only inconspicuous mesal pads, fig. 29 3

   Saw with annuli 3 and 4 either parallel or no more divergent than in fig. 4. Sheath with lateral margins low and with conspicuous mesal or ventral pads, fig. 28 6

3(2). Annulus 2 parallel with 1, figs. 5, 8 4

   Annulus 2 divergent from 1, figs. 6, 7 5

4(3). Annuli 2 and 3 far apart, fig. 5 ***hetricki*** n. sp.

   Annuli 2 and 3 close together, fig. 8. Distribution: Tex., Ala., S. C., Va., Del. Known hosts: *Pinus echinata*, *taeda*, and *rigida serotina* ***exitans*** Rohwer

5(4). Annuli 2 and 3 more oblique, fig. 7; scopa of sheath fairly thick and only moderately high. Distribution: Southeastern Canada, Wisc. Known host: *Pinus banksiana* ***swainei*** Middleton

   Annuli 2 and 3 less oblique, fig. 6; scopa of sheath thin and very high. Distribution: Me., Mass., N. J., N. Y. Known host: *Pinus rigida* ***pini-rigidae*** (Norton)

6(2). Head and thorax entirely red, abdomen with dorsum mostly blue-black 7

   Either head and thorax marked with dark brown areas or abdomen brown or rufous 8

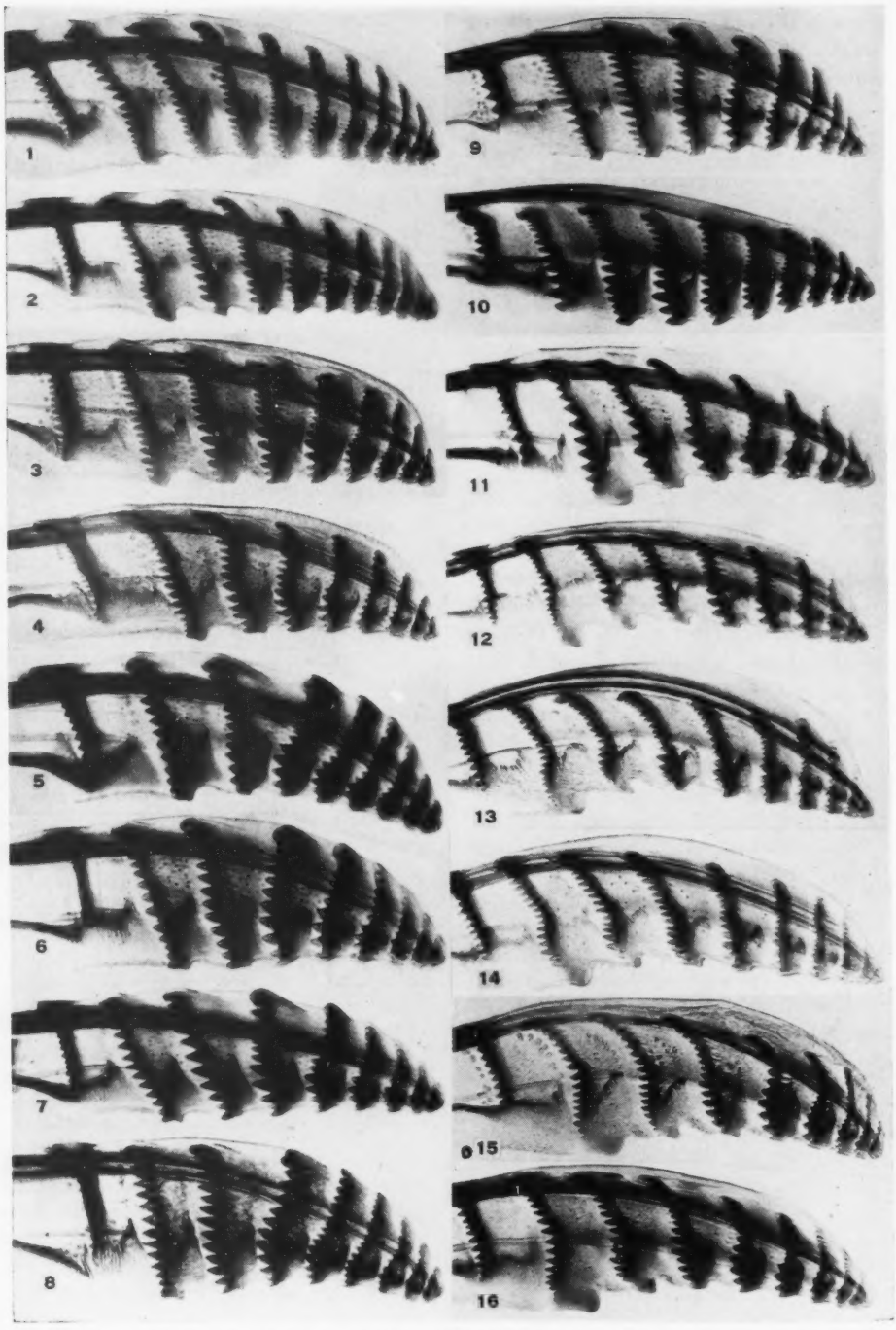
7(6). Lancet with first annulus having about 10 coarse teeth, and with ventral lobe of second annulus somewhat rounded or triangular, fig. 31. Known only from Cuba ***insularis*** (Cresson)

   Lancet with first annulus having about 14 finer teeth, and ventral lobe of second annulus rectangular, fig. 30. Distribution: Common throughout eastern continental North America. Hosts: many species of *Pinus* ***lecontei*** (Fitch)

8(6). Lancet with tractium merging into sclerora at first annulus; first annulus short, having only about 6-8 teeth, figs. 9-10 9

   Lancet with tractium ending in a definite break before first annulus; first annulus usually longer, and usually having 10 or more teeth, figs. 1-4 10

[1]Unless otherwise specified, characters refer to the adult female.



FIGURES 1-16. Lancets (lower saw blades) of Neodiprion. *1*, taedae linearis; *2*, maurus; *3*, virginicus; *4*, pinetum; *5*, hetricki; *6*, pini-rigidae; *7*, swainei; *8*, excitans; *9*, abbotii; *10*, nigroscutum; *11*, gillettei; *12*, edulicolus; *13*, demoides; *14*, nanulus contortae; *15*, sertifer; *16*, ventralis.

9(8). Annulus 2 with normal ventral tooth, fig. 9. Thorax light brown with a few linear black stripes. Distribution: Ont., Wisc., Va., N. C., S. C., Ga., Fla. Known hosts: *Pinus carribea, echinata, heterophylla, palustris, resinosa* and *taeda* ..... ***abbottii*** (Leach)

Annulus 2 short, with ventral tooth not projecting beyond membrane, fig. 10. Thorax chiefly dark brown to black. Known only from Ont., on *Pinus banksiana* ..... ***nigroscutum*** Middleton

10(8). Head and dorsum of body chiefly black, at most with reddish or piceous areas around mouth and vertex; and whitish area on scutellum 11

Ground color either rufous on head, reddish on thorax or rufous on abdomen; sometimes predominantly brown or red 12

11(10). Lancet with annulus 1 far from annulus 2, and annuli 3-5 bearing relatively large teeth, as in fig. 3. Distribution: Ont., Que., N. B., Va., N. C., Ga. Known hosts: *Pinus banksiana* and *resinosa* ..... ***compar*** (Leach)

Lancet with annulus 1 much closer to annulus 2, and annuli 3-5 bearing smaller teeth, fig. 1 14

12(10). Lancet with annuli 3, 4 and 5 sinuate, annulus 4 as parallel with 5 as with 3, fig. 4; having 8-10 annulets. Distribution: Northeastern and north-central U. S. A. and adjacent areas of Canada. Known host: *Pinus strobus*, especially in ornamental plantings ..... ***pinetum*** (Norton)

Lancet with annuli 2, 3 and 4 parallel, divergent from 5, and one or two of them straight; having 10 or 11 distinct annuli, figs. 1-3 13

13(12). Ventral lobe of annulus 2 about the same size as that of annulus 3, fig. 3; lancets with basal four annuli relatively far apart and large toothed ..... ***virginianus*** complex

Ventral lobe of annulus 2 usually larger than that of 3, fig. 2; lancet with basal four annuli closer together and finer toothed 14

14(11). Larva with red head 15

Larva with black head 16

15(14). Dorsum of female reddish with the exception of isolated dark marks on the thorax. Larva with supraspiracular band broken into a series of well-separated spots ..... ***taedae taedae*** n. sp.

Dorsum of female with thorax chiefly dark brown or black and with basal half of abdomen dark brown or black. Larva having supraspiracular band solid and dark ..... ***taedae linearis*** n. subsp.

16(14). Female having head and abdomen mostly black. Larvae with supraspiracular spots which are usually partially or entirely atrophied in middle of trunk. Occurring in the eastern states from Maryland to Maine ..... ***pratti paradoxicus*** n. subsp.

Either female abdomen and head usually mostly rufous, or larvae with supraspiracular line solid or nearly so, or occurring west of the above area 17

17(16). Most of the population with dorsum of body chiefly dark brown or black, and head with

a black band between vertex and lower part of face..18
Most of population with head and dorsum various shades of light brown. Distribution: Southern Canada from N. B. to Man.; Mich., Wisc., Minn. Hosts: Primarily *Pinus banksiana*, occasionally on other species ..... ***pratti banksianae*** Rohwer

18(17). Overwinters in egg stage. Larva with lateral stripes. Distribution: Va., Md., Ind. Known host: *Pinus taeda* ..... ***pratti pratti*** (Dyar)
Overwinters in prepupal stage. Larvae with lateral spots. Distribution: Wisc., Minn., and southeastern Canada. Known host: *Pinus banksiana* ..... ***maurus*** Rohwer

19(1). Female with head and entire body bluish black, sometimes with a suffusion of deep reddish black on dorsum of head and part of abdomen. Saw, fig. 11, with ventral tooth of annulus 3 quadrate and large and only little "stepped down" from lobe of annulus 2. Distribution: Colo., N. Mex. Known host: *Pinus scopulorum* ..... ***gillettei*** (Rohwer)
Either female head and body with some light brown areas or saw with ventral lobe of annulus 3 considerably stepped down from that of annulus 2, fig. 12 20

20(19). Ventral lobes of annuli 2 and 3 both large, that of annulus 3 only slightly oblique and little stepped down from lobe of annulus 2, figs. 17-18 21
Either ventral lobes of annuli 2 and 3 smaller and markedly oblique, fig. 19, or that of annulus 3 much smaller and considerably stepped down from that of annulus 2.....22

21(20). Teeth of annulus 3 very large and coarse, similar to those of annulus 4, fig. 18 ..... ***werneri*** n. sp.
Teeth of annulus 3 much smaller than those of annulus 4, fig. 17. Distribution: Wash. Type labeled "On Fir." ..... ***scutellatus*** Rohwer

22(20). Ventral lobe of annulus 2 small, as in figs. 19, 20, often not much larger than that of annulus 3, and its margin round or oblique 23
Ventral lobe of annulus 2 massive, much larger than that of annulus 3, fig. 12 26

23(22). Ventral lobe of annulus 2 projecting greatly from base of ventral margin in comparison with lobe of annulus 3, as in fig. 12. On *Pinus* 26
Ventral lobe of annulus 2 projecting only slightly more than that of annulus 3, figs. 19, 20. Not on *Pinus* 24

24(23). Processes of scopa not or only slightly oblique, fig. 26.....25
Processes of scopa markedly oblique, fig. 27. Distribution: Northern and transcontinental. Known hosts: *Abies*, *Picea*, *Pseudotsuga*, *Tsuga* ..... ***abietis*** complex

25(24). Annuli 4-6 having uniform and very large teeth, much larger than those on annulus 3, fig. 10. On *Abies* ..... ***deleoni*** n. sp.
Annuli 4-6 having either small teeth or with the more ventral teeth much larger than the dorsal group, as in fig. 20. Distribution: Alaska, B. C. Known host: *Tsuga* ..... ***tsugae*** Middleton

26(22, 23) Occurring east of the 100th meridian 27
Occurring west of the 100th meridian 28

27(26). Front wings with R+M black, R from origin to stigma bright brown; lancet 9-segmented, with last three close together, annuli 5-7 with marginal tooth not overlapped by others in same row, fig. 15. Distribution: N. Y. and southern Canada westward to Ill.; introduced from Europe. Known hosts: *Pinus echinata, resinosa, rigida,* and occasionally other species ..... ***sertifer*** (Geoffroy)
Front wings with R+M black, and R to stigma dark brown; lancet 9-segmented, the last three well separated, annuli 5-7 with marginal tooth overlapped by one or two in same row. Distribution: SE Canada and NE United States, west to Man. and Wisc. Known hosts: *Pinus banksiana* and *resinosa* ..... ***nanulus nanulus*** Schedl

28(26). Lancet with annuli 3 and 4 ending below rod and at apex curved sharply basad, fig. 13 ..... ***demoides*** n. sp.
Lancet with annuli 3 and 4 extending on or over rod and not curving sharply at apex, figs. 12, 14 29

29(28). Dorsum mostly black; head with at least a black frontal band 30
Dorsum consisting of a light or medium brown ground color with dark markings superimposed, or head red or yellow 31

30(29). Venter and legs light, nearly yellow ..... ***ventralis*** n. sp.
Venter and legs much darker. Distribution: Calif., Ore. Known host: *Pinus ponderosa* ..... ***mundus*** Rohwer

31(29). Scopa very short, fig. 24, 1:3 compared with base; lancet unusually narrow; annuli 3 and 4 short dorsally, fig. 12. Body small and pale with dark vittae on mesonotum ..... ***edulicolus*** n. sp.
Either scopa longer, fig. 25, or lancet wider, fig. 14. Color various 32

32(31). Larger species, female about 10-11 mm. long. Distribution: Throughout western montane region. Chiefly on *P. ponderosa* ..... ***fulviceps*** complex
Smaller species, female about 7-9 mm. long. On *P. contorta* 33

33. Annuli 3-5 with teeth as fine as those on annulus 2, fig. 14 ..... ***nanulus contortae*** n. subsp.
Annuli 3-5 with teeth coarser than those on annulus 2, much as in fig. 16. Distribution: Wyo. ..... ***burkei*** Middleton

Notes on Critical Species

References to original descriptions and the more important literature have been published previously (Ross, 1951) and are not repeated here. The status of certain names has changed and certain forms appear to be undescribed. These matters are treated in this section. Where numbers permit, paratypes of new species are deposited in the U. S. National Museum, the Illinois Natural History Survey, the University of Wisconsin, the Canadian National Museum, and the University of Toronto.

Neodiprion pini-rigidae (Norton)

Previously this species went under the name *fabricii* (Leach), but the name *fabricii* actually applies to another species and is a synonym of *abbotii.*

Previously four names were considered

synonyms of this one. It is now apparent that *pini-rigidae* belongs to a complex of four closely related species. The name *akhursti* (Norton) is a synonym of *pini-rigidae*, but *swainei* Middleton and *excitans* Rohwer represent valid species in addition to a fourth, *hetricki*, here described as new. In the larva the head is black in all but *swainei*, in this species varying from black to red. The larvae of all species have the subdorsal dark line solid, but the supraspiracular dark band varies from a solid line to various spotlike reductions.

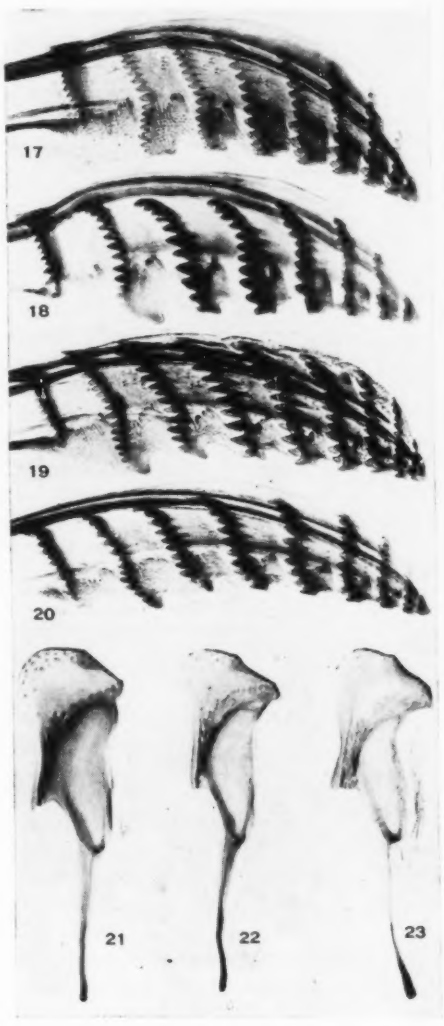
Neodiprion hetricki new species

Female.—Length 9 mm. General color yellowish-brown with the following parts blackish-brown: antennae, eyes, ocellar area, antero-mesal triangle of praescutum, most of scutal lobes, and most of dorsum of abdomen. Antennae 18-segmented. Sheath with thin scopal processes which are moderately high and have their apices curved mesad, fig. 29. Lancet of saw as in fig. 5; annuli 1, 2, and 3 parallel and spaced far apart, annulus 4 divergent from 3, and the entire apical portion of the lancet canted at a marked angle to the base. *Male.*—Length 8 mm. Color and general structure typical for genus. Penis valve with apical cap fairly high and narrow, much as in fig. 21.

Holotype female and allotype male.—Caroline Co., Va., Oct. 13, 1941, reared from *Pinus taeda*, L. A. Hetrick (Type No. 62758, U. S. N. M.). Paratypes.—Same data as holotype, except for different emergence dates in October, 57 ♀, 22 ♂; Mathews Co., Va., Oct., 1941, reared from *Pinus taeda*, L. A. Hetrick, 29 ♀, 12 ♂.

In the larva of this species the head and anal patch are black, the subdorsal band is solid, and the supraspiracular band is either composed of separate spots or these are coalesced to form a beaded line.

From the other three members of the *pini-rigidae* complex, *hetricki* may be distinguished by the widely-separated but parallel annuli 1, 2, and 3 of the female lancet. To date, diagnositic characters have not been found to separate males of these species.



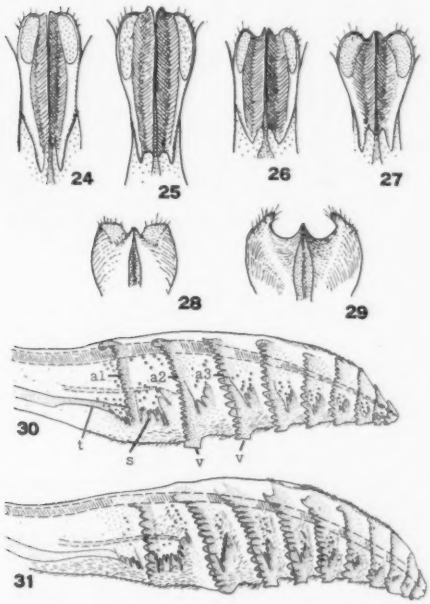
FIGURES 17-20. Lancets of Neodiprion. *17*, scutellatus; *18*, werneri; *19*, deleoni; *20*, abietis.

FIGURES 21-23. Penis valves of Neodiprion. *21*, nanulus contortae; *22*, deleoni; *23*, abietis.

Neodiprion abbotii (Leach)

Leach in 1817 described from Georgia three light-colored species of *Neodiprion*, *abbottii*, *americanus*, and *fabricii*, and for many years entomologists guessed at their identity. In 1952 I was able to examine the types of these names and found that all three belonged to the species previously recorded as *rileyi* (Cresson). It is therefore necessary to make an extensive shift in names (see also *pini-rigidae* and *taedae*). All three of the Leach names occur on the same page and *americanus* has line priority. I am taking the reviser's prerogative and select *abbotii* as the accepted name because in this way much confusion will be avoided.

As pointed out by Atwood and Peck (1943) this species is readily diagnosed in the larva by the pale spot on the front of the dark head.



FIGURES 24-27. Saw sheaths of Neodiprion, *ventral aspect. 24*, edulicolus; *25*, nanulus contortae; *26*, deleoni; *27*, abietis.
FIGURES 28, 29. Saw sheaths of Neodiprion, *dorsal aspect. 28*, pinetum; *29*, hetricki.
FIGURES 30, 31. Lancets of Neodiprion. *30*, lecontei; *31*, insularis. *a1*, *a2*, *a3 annuli 1, 2, and 3 of lancet*; s, *sclerora*; t, *tangium*; v, *ventral lobes.*

Neodiprion nigroscutum Middleton

There seems to be no doubt that this species, synonymized with the preceding in 1951 by Ross, is a valid specific unit. According to Atwood and Peck (1943), the larva probably has a black head without a frontal light spot.

Neodiprion pratti (Dyar)

Neodiprion dyari Rohwer, 1918. Ent. Soc. Wash. Proc., 20:85. *N. syn.*

The lone female type of this species has been an enigma for many years but recently rearings by Dr. Hetrick have offered a solution to the problem. Dr. Hetrick has reared a large series of dark females from *Pinus taeda* in Virginia, near the type locality of *pratti*, and with some members of this series the types of both *pratti* and *dyari* match exactly. It seems certain, therefore, that *pratti* is the prior name for this variable, common species formerly called *dyari*.

The species as a whole can be divided into three geographic units, each differing from the others in average characters which are almost absolute. Until more knowledge of the complex indicates a better solution, it is proposed that these three segregates be considered as subspecies. These include the subspecies *pratti* (Dyar), *banksianae* Rohwer, and *paradoxicus* n. subsp., all diagnosed in the key.

This species is remarkably similar morphologically to *taedae*, including a practically identical saw. The two species occur together but remain distinct at least in Virginia, which indicates that the two are completely distinct biological entities.

Neodiprion pratti paradoxicus n. subsp.

Female.—Length 8 mm. Head reddish but with a black band extending between the eyes across the ocellar area. Body

chiefly brownish black above, brownish yellow below, with some of the dorsal thoracic sclerites brown and with the middle of the femora blackish. *Larva.*—Head black. Body with unusually pale subdorsal stripes; supraspiracular stripe represented only by a series of dark spots which are usually atrophied in the central body region.

Holotype female and allotype male.—Orange, Mass., Sept. 29, 1941 (364-205-41-3), reared from *Pinus rigida* (Type No. 62759, U. S. N. M.). Paratypes.—Large series of specimens from Ashby, Holyoke, New Salem, Orange, and Uxbridge, Mass., and Litchfield, Conn., all reared from *Pinus banksiana* or *rigida*.

Neodiprion taedae taedae n. sp. and subsp.

Female.—Length 8 mm. Color pale brownish yellow with antennae, eyes, and a few thoracic markings black. Sheath with low scopal pads. Lancet, as in fig. 1, having annuli 2-4 parallel, with small teeth, and with ventral lobe of annulus 2 much larger than that of annulus 3. *Male.*—Length 7 mm. Color chiefly black, in general structure typical for genus. *Larva.*—Head red. Body with solid subdorsal dark stripe, but with supraspiracular stripe broken into isolated dark marks; terminal segment with large, divided dark patch.

Holotype female and allotype male.—King and Queen Co., Va., Oct. 13, 1939, L. A. Hetrick (Type No. 62760, U. S. N. M.). Paratypes.—King and Queen Co. and Matthews Co., Va., L. A. Hetrick, all reared from *Pinus taeda*, 32 ♂, 22 ♀.

This species has been described by Hetrick (1941) under the name *Neodiprion americanum* (Leach). The type of *americanum* proves to be an entirely different species, hence a new name is necessary for this common loblolly pine sawfly. Hetrick records it from *Pinus taeda* and *echinata*, and as an occasional on *Pinus virginiana*. This typical form has been found to date only in Virginia.

Neodiprion taedae linearis n. subsp.

Female.—Similar in structure to *taedae taedae*. Color averaging much darker, the scutal lobes, anterior half of praescutum and dorsal bands on the basal segments of the abdomen usually black. *Larva.*—Differing from *taedae taedae* in having the supraspiracular stripe solid on all but the two or three posterior segments, and in having the dark dorsal patch on the last segment either with a lighter central area or not at all in evidence. All forms have been taken in the same area. On very dark specimens there are two more slender dark stripes through and below the spiracular area.

Holotype female and allotype male.—Urania, La., Ap. 2, 1954, (as larvae), on *Pinus taeda*, F. J. Coyne (Type No. 62761, U. S. N. M.). Paratypes.—Same data as for holotype and from Fordyce, Ark., all reared from *Pinus taeda*, 100 ♂, 50 ♀.

In addition to these localities, larvae of this subspecies have been collected from Fayetteville, Ark., and Daisetta, Tex.

Neodiprion virginicus complex

On the basis of lancet structure, females of this complex fall into two categories. In one the first annulus is long and bears a dozen or more teeth, fig. 3, and in the other the first annulus is short, exactly as in *abbotii*, fig. 9. The former type seems to predominate in the southeastern portion of the range, the latter in the northern and western portions. The color of the larval head also varies from black to reddish-black. Detailed studies of reared populations from all parts of the range will be necessary to determine whether one or two distinct species or races are involved in this complex. The names to be considered are those listed under *virginicus* Rohwer by Ross (1951). The larvae are indistinguishable from those of the *taedae* and *pratti* complex.

Neodiprion werneri n. sp.

Female.—Length 7.5 mm. Color light brownish yellow throughout with the following small areas black: Eyes, antennae, narrow lines on scutal lobes, and narrow sclerites at the base of the abdomen. General structure typical for genus. Sheath with scopal pads flaring moderately, as in fig. 25. Lancet of saw deep and short, tapering conspicuously toward apex, fig. 18; ventral lobe of annulus 1 projecting only moderately beyond that of annulus 3; annuli 3, 4, and 5 with very large teeth, annuli 3 and 4 with upper ends curving toward base; annulus 7 is only about 2/3 as long as annulus 6.

Holotype female.—Hospital Flat, Pinelino Mountains, Arizona, collected in meadow in spruce-fir zone, 9000 feet elevation, August 8, 1949, Werner and Nutting (Illinois Natural History Survey collection).

Closest to *scutellatus*, this species differs in having much larger teath on the third annulus, a shorter annulus 7, and the more protecting ventral lobe of annulus 3. The flared sheath of *werneri* resembles that of *abietus*, but the saws of the two species are quite different.

Neodiprion deleoni n. sp.

Female.—Lengh 8 mm. Color light yellowish brown with the following small areas black: eyes, antennae, linear streaks on the lateral lobes of the scutum, and sclerites at the base of the abdomen. General structure typical for genus. Sheath with scopal pads of moderate length, fig. 26. Lancet of saw with ventral lobe of annulus 2 projecting conspicuously but only slightly larger than that of annulus 3; both of these ventral lobes have the ventral margin oblique; annuli 2-6 regularly spaced and parallel; annuli 4, 5, and 6 with unusually large and even teeth compared with those of annuli 2 and 3; annulus 7 nearly as long as 6; lancet moderately deep for its whole length, fig. 19. *Male.*—Similar in color and general structure to other members of the genus. Hood of penis valve slightly more hoodlike than in previously mentioned species.

Holotype female and allotype male.—North Port, Washington July 5, 1930, reared from *Abies grandis*, D. DeLeon (Hopkins No. 19934) (Type No. 62765, U. S. N. M.). Paratypes.—Same data, 4 ♀, 4 ♂.

This species is most closely related to *werneri*, but differs in the oblique ventral lobes of annuli 2 and 3.

Neodiprion abietis complex

Field workers have reported that material of this complex reared from *Picea* seems biologically different from material on *Abies*, yet the adults of the types appear indistinguishable. In western North America adults reared from *Pseudotsuga* and *Tsuga* differ slightly in size, color, and somewhat variable saw characters from series on *Abies* and *Picea*. It seems evident that much careful rearing needs to be done before we will know how many distinct biological and genetic units are involved in this complex.

Neodiprion demoides n. sp.

Female.—Length 8.5 mm. Color pale yellow-brown, the eyes black, the antennae and a stripe on each lobe of the scutum, brownish black. General structure typical for genus. Scopa narrow and fairly long, as in fig. 25. Lancet, fig. 13, with annulus one short, the ventral lobe of annulus 2 projecting conspicuously, and having annuli 3 and 4 with their upper margins curved basad and ending below rod. Annuli 5 and 6 are also relatively short. Annuli 4, 5, and 6 have the ventral teeth larger than the others. *Male.*—Color and structure typical for other species of the genus.

Holotype female and allotype male.—Yosemite National Park, California, October 1934, reared from *Pinus albicaulis* (364), D. DeLeon (Type No. 62763,

U. S. N. M.). Paratypes.—Same data as for holotype, 1 ♀, 4 ♂.

The larva has a black head; the trunk is also chiefly black, with a narrow dorsal white line and two narrow lateral pale lines, all three presumably light green in life. The spines on the cauda are conspicuous and heavy as in *sertifer*.

Neodiprion ventralis n. sp.

Female.—Length 10 mm. Color of most of head, legs and all of venter of body, pale yellowish brown; the following parts are black: eyes, antennae, a conspicuous band on the head extending from eye to eye just above the antennae, most of the dorsum of the thorax, and all but the apex of the dorsum of the abdomen. General structure typical for genus. Sheath with scopal pads of moderate length, as in fig. 25. Lancet of saw with ventral lobe of annulus 2 large and massive, that of annulus 3 of moderate size, and with its ventral margin quadrate; teeth throughout the saw moderately coarse, the ventral group on annuli 4, 5, and 6 larger than the others; apical portion of lancet moderately long and narrow, fig. 16. *Male*.—Similar in color and general structure to other members of genus.

Holotype female and allotype male.—Plain View, Colorado, October 1, 1935, reared from *Pinus ponderosa*, J. A. Beal (Hopkins No. 17700-D) (Type No. 62764, U. S. N. M.). Paratypes.—Same data, one female; Boulder, Colorado, September 27, 1933, four females, one male.

This species is most closely related to *fulviceps*, from which it differs in the dark band on the head of the female and in the quadrate ventral tooth of second annulus of the lancet.

Neodiprion edulicolus n. sp.

Female.—Length 8 mm. Color light yellowish brown, the eyes black, antennae, a narrow ocellar line, center of praescutum, and small areas of the scutal lobes, brownish black. General structure typical for genus. Sheath with unusually short scopal pads, fig. 24. Lancet of saw with ventral lobe of annulus 2 projecting conspicuously more than that of annulus 3; annuli 4, 5, and 6 usually with the ventral teeth larger than the others, fig. 12. *Male*.—Similar in color and general structure to other members of genus.

Holotype female and allotype male.—Colo.-N. Mex. line, Colo., Oct., 1936, D. DeLeon, on *Pinus edulis*, 744 (Type No. 62762, U. S. N. M.). Paratypes.—Same data, 8 ♀, 9 ♂.

A female from Zion N. P., Utah, on *Pinus edulis* (Hopkins No. 34215-5), also belongs to this species. The larva is not available.

Neodiprion mundus Rohwer

Larvae of this species have been secured from *Pinus ponderosa* near Corvallis, Ore. In the last feeding stage, the head of the larva is yellow with the frontal area black and the area around the mouth yellowish; the dark body bands are only moderately dark and of moderate width, so that there is a wide light area along each side of the body. In earlier larval instars the head is almost entirely black.

Neodiprion fulviceps complex

Large numbers of collections from *Pinus ponderosa* provide the most puzzling questions in this genus. It is possible that all these are a single species, perhaps represented by a number of fairly well-marked geographic races. If so the name *fulviceps* (Cresson), described from Nevada, might apply. The variation encountered in color and saw characters of the adults, however, makes a conclusion impossible at this time. The problem is further complicated by differences in the larvae. Larvae associated with different rearings of light colored adults have heads which are black (as in *burkei*), red, or red with a black frons (much as in *mundus*).

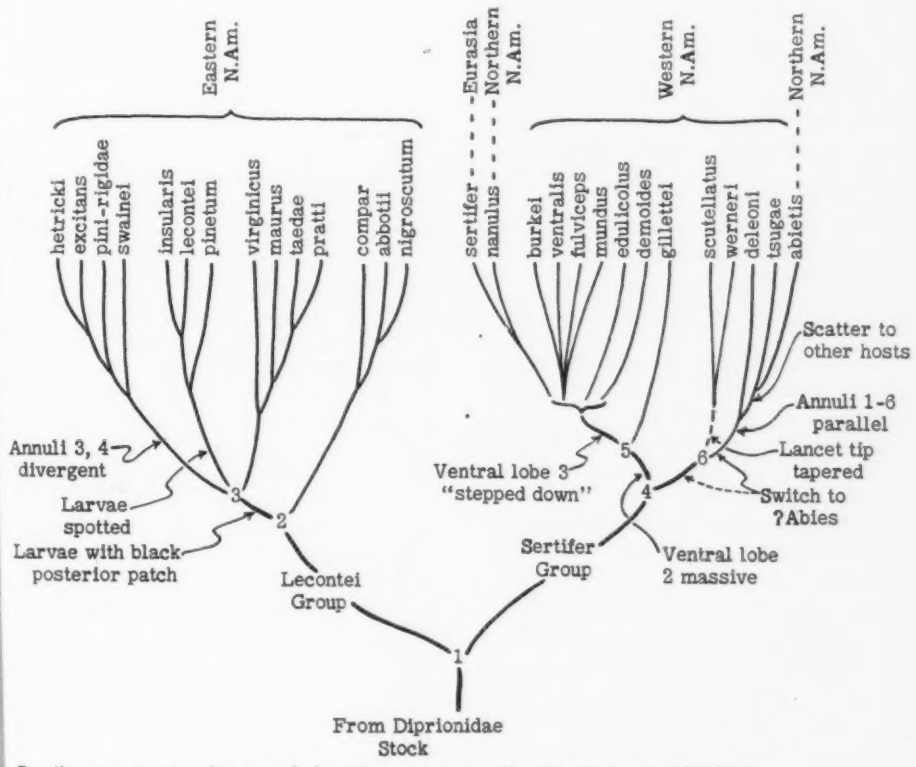
Neodiprion nanulus contortae n. sp.

Several series reared from *Pinus contorta* in Oregon are virtually identical with eastern series of *nanulus* in color range and structure of both adults and larvae, and also in passing the winter in the egg stage (see Atwood & Peck 1943). There seems no doubt that only a single species is involved. The Oregon and other western populations differ from eastern populations in having slightly finer teeth on annuli 3 and 4 of the lancet, fig. 14. According to existing records the two populations are separated by a wide gap extending from western Alberta to eastern Manitoba. The western populations are therefore considered as a distinct subspecies *contortae*.

Holotype female and allotype male.—McKenzie Pass west of Bend, Ore., cocoons collected from *Pinus ponderosa* station Jn. 23, adults emerged Sept. 10-21, 1954, F. P. Keen and R. L. Furniss (Type No. 2676, U. S. N. M.). Paratypes. —Same data, 21 ♂, 94 ♀. Additional records are from Cascade, Id., Kirk, Ore., and Jasper, Alta., all reared from *Pinus contorta*.

Evolution of Neodiprion

In comparing both adults and larvae of the reared species of *Neodiprion* with each other and with other genera of Diprionidae, it is evident that our present members of *Neodiprion* arose from an ancestor possessing (1) lancets in which the annuli were



Family tree showing known relationships and geographic distribution of Neodiprion.

subparallel and the ventral lobes of annuli 2 and 3 were about equal in size, and (2) larvae in which both the subdorsal and supraspiracular dark lines were uninterrupted and the posterior segment had no well-delineated dark patches. From such a form (Ancestor 1 of the accompanying chart) two lines arose, one giving rise to the parent of the *sertifer* group, with minute-punctured mesoscutellum (Ancestor 4), the other to the parent of the *lecontei* group, with coarsely pitted mesoscutellum (Ancestor 2). Of existing members of the *lecontei* group the *abbotii* complex appears to be the most primitive offshoot, its larva having at most an indistinct posterior patch. From Ancestor 2 arose a second group in which a posterior patch developed in the larva, as well as a potentiality for the supraspiracular dark line to break up into patches. From such a form (Ancestor 3), three complexes arose, the *lecontei* complex is which the subdorsal line of the larva also broke up into patches, the *pini-rigidae* complex in which annuli 3 and 4 became greatly divergent, and the *pratti* complex which remained primitive in both characters.

The line of the *sertifer* group appears to have divided into two branches. In one of these the ventral lobe of annulus 2 became more massive and the succeeding lobes became smaller, resulting in a "step-down" appearance. Beyond identifying *gillettei* as the most primitive known member of this branch, it is difficult to do more than suggest affinities between a few species. In the other branch, leading to *abietis*, there is a definite trend in the saw toward a more parallel condition of the annuli and smaller ventral lobes, and in the penis valves to a more hooded condition, figs. 22, 23.

Because of the pine-feeding nature of allied genera such as *Zadiprion* and *Diprion*, and of the entire *lecontei* group and one branch of the *sertifer* group, it is logical to conclude that Ancestors 1 and 4 also fed on *Pinus*. It seems, therefore, that Ancestor 6, or the *abietis* line just beyond it, was the first and only line of the genus to become established on another host, possibly *Abies*. After this jump several others were made, to *Tsuga*, *Pseudotsuga*, and *Picea*. The most specialized species in this line, *abietis*, is the only species in the genus known to feed on several genera.

Dispersal of Lines

An examination of the areas inhabited by the various species and complexes indicates that

(1) since all the species of the *lecontei* group occur only in eastern North America, it is highly likely that Ancestor 2 was an eastern segregate of a widespread Ancestor 1, and that the entire evolution of the *lecontei* group occurred in this area; and

(2) since all but one member of the *sertifer* group occur in western North America, and of these all the primitive forms are restricted to that area, it is probable that Ancestor 4 was a western segregate of Ancestor 1, and that the chief evolution of the group occurred in the West.

The species *sertifer* represents the only known dispersal of the genus presumably from western North America to eastern Asia and ultimately across Eurasia. From Europe, via man's agency, it was introduced into eastern North America.

The only two known cases of American transcontinental dispersal in the *sertifer* group indicate that the event took place at a relatively recent date. In the case of *nanulus* the eastern and western populations are virtually identical morphologically, with a slight average difference between them. Furthermore, they feed on the only two species of pine whose ranges actually overlap to form an east-west pine bridge. In the other case, the spruce populations of the species *abietis* appear to be identical from west to east, and they have a well established host bridge across the northern coniferous forest. Both cases can be explained best as species which evolved in the West and spread to the East sufficiently recently

that there has been no opportunity for the isolation and evolution of the eastern populations to form distinct species.

The total of this evidence indicates that, during most of the period of *Neodiprion* evolution, there existed a complete barrier to the transcontinental dispersal of the group, and that only an occasional species (apparently only the most northern) was ever able to spread from one major area to another. Ancestor 1, of course, must have dispersed across the continent, but it would appear that after this a long period elapsed before another such dispersal occurred.

Correlation with Forest Evolution

These probable events in *Neodiprion* were undoubtedly correlated with corresponding conditions in their host. On the basis of data from other groups (Ross 1953), the best explanation which can be inferred at this time suggests the following sequence of events for the pine forests and sawflies which fed on them.

1. In mid-Tertiary (possibly early Miocene, some 40 or 50 million years ago), the mesic forests were world wide, and at this time the *Neodiprion* progenitor spread with its pine hosts across North America.

2. During the later part of the Tertiary, the upward movement of the western mountain areas caused a change in climate resulting in the formation of a more arid Great Plains region. This region developed into a grassland area, and the forest area became broken into eastern and western regions. During this period the biotas of the two forest areas would evolve independently.

3. During the Pleistocene conditions changed so that an occasional species of *Neodiprion* (and presumably also of *Pinus* and other genera) was able to spread from one area to another.

This latter can be readily visualized if one consults range maps of the pines (Munns, 1938; Morton, 1949). Of the nearly 30 species of pines in North America, all but one occur in either the western or the eastern forest areas. Only *Pinus banksiana* extends across the continent from one area to the other. If the present glacial retreat continues much farther, the northern extension of the Great Plains would cut the range of this pine into an eastern and a western portion just as it would cut the range of *Neodiprion abietis*.

It must be emphasized that these are preliminary attempts to explain these phenomena of relationships and distribution. It is certain that more detailed knowledge of both, not only for *Neodiprion* but also for its hosts, will add much to our understanding of past geological events and perhaps to our ability to predict the future.

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Mineral Composition of the Foliage in Relation to the Growth of Scots Pine

BY

L. LEYTON

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THE NUMEROUS REPORTS of pronounced responses in tree growth to the application of mineral fertilizers suggest that such measures may possess distinct economic advantages in the amelioration of low quality forest sites. The problem arises as to how the nature and extent of existing mineral deficiencies may best be established. The direct approach of setting up field trials with various levels and combinations of fertilizers is time consuming and expensive. Nor have soil analyses proved as reliable in the assessment of site fertility for forest trees as perhaps for agricultural crops. With these difficulties in mind, many investigators have turned to foliar analysis in the hope that the mineral composition of the foliage might provide a more reliable guide to the presence and extent of a particular mineral deficiency.

The simplest and most common application of foliar analysis is based essentially on comparisons between normal healthy trees and trees suspected of being mineral deficient, on the assumption that a lower concentration of a particular nutrient in the latter indicates a deficiency in that nutrient. This method has been used to a considerable extent by Nemec (1938, 1940, 1942) and others, in the diagnosis of mineral disturbances assumed responsible for the poor growth of trees in established stands. Its validity depends to a large extent on whether suitable standards of comparison representing "normal" concentrations of the various nutrients can be established for that particular species; from a practical point of view it also requires that, over the deficient range at least, the concentration of a nutrient in the foliage and its availability in the soil are both positively related to growth.

A considerable amount of attention has been devoted to the concept of normal or optimal concentrations of particular nutrients, especially in connection with the establishment of sub-optimal or minimum concentrations corresponding to deficiency conditions but the situation is still rather controversial (Goodall and Gregory, 1947). It is generally recognized that the mineral composition of the foliage of trees is influenced not only by the availability of nutrients in the soil but also by the age of the tree, the age of the foliage (i.e. in conifers bearing more than one year's foliage), the location of the foliage in the crown and the time of sampling (for a review of these factors cf. Leyton, 1948; White, 1954; Tamm, 1955). Recognition of these sources of variation has led to the adoption of standardized techniques involving comparisons of foliage sampled at the same time from trees of similar age.

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Almost universal agreement has been reached in sampling current foliage collected at the end of the growing season when variation in composition with time is at a minimum. As yet there appears to be no generally accepted scheme for the location of samples in the crown; certain investigators prefer an average value representing the whole crown (Wallihan, 1944; White, 1954) whilst others restrict sampling to a particular position in the crown (Mitchell and Chandler, 1939; Leyton, 1954). Experimental evidence as to the relative merits of the different sampling methods for agricultural and horticultural crops has usually been based on proportional differences between plants at different levels of nutrition (Goodall and Gregory, 1947), but little information of this kind appears to be available for forest trees despite the obvious importance of this factor. The following investigation was intended in part to provide more information on this point, with the hope that the choice of material can be established on a firmer basis than would appear to exist at present.

Even if we assume that valid comparisons can be made between trees by sampling under identical conditions there still remains the problem of interpreting nutrient concentrations in terms of tree growth and nutrient availability in the soil. Because of the possibility of luxury consumption (*i.e.* nutrient uptake not accompanied by increased growth, thus leading to excessive concentrations in the tissues) a "normal" tree need not necessarily reflect optimum concentrations of the various nutrients, if such exist, so that simple comparisons between trees may lead to considerable errors in diagnosis. Furthermore there is some doubt as to the amount of significance which can be attached to the concentration of individual nutrients independent of the influence of other nutrients and of other growth factors. According to certain investigators (Macy, 1936; Ulrich, 1943) there is for each nutrient, more or less independent of other growth factors, a narrow range of concentration (so called critical level) above which there is no response and below which growth increases as the supply of that nutrient is increased. A somewhat similar approach has been adopted by Heiberg and White (1951) and by Stone (1953) for forest trees in so far as they postulate certain concentrations of potassium and magnesium in the needles which correspond to deficiency levels of these nutrients. From investigations into the response of various hardwood species on different sites to various levels of a nitrogenous fertilizer, Mitchell and Chandler (1939) also suggest certain concentration ranges of this nutrient equivalent to minimum and optimum levels. On the other hand it has been claimed for agricultural crops (Lundegårdh, 1941) that the increment in yield following a given fertilizer application to plants with a particular concentration of that nutrient is markedly affected by the level of other nutrients, whilst Thomas (1945) maintains that the question of balance between nutrients must also be taken in account.

To a certain extent these difficulties in interpretation can be avoided by extending the investigations to cover a wide range of conditions of growth and nutrient status to allow for a statistical analysis of the relationships involved. From the investigations of Mitchell (1939) and Mitchell and Chandler (1939) in which trees (or seedlings) have been treated with different levels of a particular nutrient, it would appear that over the deficient range (i.e. the range over which growth increases as the nutrient supply is increased) there is a positive relation between nutrient supply, nutrient concentration in the foliage and growth and that over a more limited range this relationship is effectively linear. Experiments in the field with rubber (Chapman, 1941) and with Sitka spruce (Leyton, 1954) would confirm that a significant linear correlation between growth and the concentration of a particular nutrient in the foliage indicates a deficiency in that nu-

trient. According to the latter investigation it would also appear that actual fertilizer trials are not always necessary to provide the required range of material; even-aged stands showing heterogeneous growth conditions may also be used though of course the ultimate proof of deductions based on this material can only be obtained by applying the particular fertilizer and noting the response in tree growth. In analyses of this kind, attention is usually restricted to one particular nutrient (usually the so-called limiting nutrient), but in view of repeated observations that growth may be increased by the application of more than one nutrient (often with pronounced interactions), it would appear necessary to extend the analyses to include a number of nutrients, ideally all nutrient factors. Although a certain amount of work has been devoted to the effect of various nutrient combinations on tree growth (cf. Van Goor, 1953), few attempts have been made to relate these responses to nutrient concentration by means of multiple regressions. A limited example of this approach is provided by Stone (1953) for potassium and magnesium in red pine, and a more comprehensive analysis by Leyton (1955) for nitrogen, potassium, phosphorus, calcium and other ash constituents in Japanese larch. A similar comprehensive analytical approach has been adopted in the present investigation with Scots pine (*Pinus sylvestris* L.).

For the most part, investigations dealing with adult trees in the field have dealt with tree height or diameter as an expression of growth vigor and response. Since in the present investigation, data are available for dry weight production of the trees besides those for height and diameter, the analysis of growth-nutrient relationships has been extended to include dry weight.

Description of Experiment

Sample trees were selected from a pure plantation established in 1945 in the Bramshill forest, Berkshire, England. The soil is a sandy heathland podzol, overlying Barton beds (Eocene) with a dominant ground vegetation of common heather (*Calluna vulgaris*, L.) with bell heather (*Erica cinerea*, L.). The plantation is approximately 300 ft. above sea level and the average annual rainfall is 25-30 inches.

Ten trees were located within a radius of approximately 150 ft. ranging in height from 4.3 to 14.0 ft.; these trees represented roughly the range in height which occurred in the plantation as a whole and, in the absence of suppression by shade, the variation in vigor might be ascribed to a combination of heterogeneity in soil conditions and planting stock and perhaps to differences in treatment during planting. On the 5th of October, 1954, one lateral branch from each of the topmost three whorls of each tree (south side) was removed. At the same time, height and basal diameter were measured. The day after sampling, all needles were removed from the main stem of each branch, separated according to age and dried in an oven at 105° C. for 48 hours. After grinding in a mill, the needles were analyzed for nitrogen, phosphorus, potassium, calcium and total ash contents. using more or less conventional methods of analysis.

Two weeks after the initial sampling, each tree was cut at ground level for the determination of total dry weight. At the same time further needle samples were taken for analysis from the leading shoot of each tree.

Results

The range in concentration covering the ten sample trees for each nutrient and for each position of sampling is given in Table 1. An attempt has been made to estimate ash constituents other than P, K and Ca by subtracting from the total ash contents, values equivalent to P_2O_7, K_2CO_3 and CaO. In the absence of precise information as to the composition of the ash, the resulting "ash residue" must of course be treated only as an approximation.

These findings more or less agree with those of previous investigators as far as the effect of location and age on needle composition is concerned (Nemec, 1948; White, 1954). With current needles the highest nutrient concentrations were generally found in the terminal shoots, but there were no consistent differences between shoots lower down the crown. With increasing needle age nutrient concentrations tended to fall except in the case of calcium and ash residue which reached their highest concentrations in the older needles.

The relationship between needle composition and tree height. Linear correlations have been calculated between tree height and the concentration of each nutrient for each needle sample; the corresponding correlation coefficients are given in Table 2.

Inspection of these coefficients indicates in a number of cases, significant linear relationships (or linear components of the relationships) between tree height and nutrient concentration in the needles. For the current needles from the uppermost shoots there is evidence for a linear relation with more than one nutrient (e.g. in the terminal shoot, with N, P and K) whereas for the lowest whorl sampled (Whorl 3) only one nutrient, Ca, is possibly related to height. With the exception of potassium, there is little evidence for such relationships in the case of the older needles.

In those cases where the linear correlation closely approaches or exceeds the 5 percent level of significance, the coefficient (b) for the linear regression of nutrient concentration on tree height has been calculated and the values also given in Table 2.

It is evident from these regression coefficients that, as far as nutrient concentration

TABLE 1. Range in concentration of nutrients in pine needles of different age sampled from various parts of the crown of trees of different height. All results expressed as percentage dry weight.

Needle Age	Location of Shoot[1]	N	P	K	Ca	A[2]
Current	Terminal	1.26-1.76	.14-.21	.73-1.46	.25-.39	.24- .63
Current	Whorl 1	1.06-1.39	.11-.16	.65-1.08	.19-.30	.09- .84
Current	Whorl 2	1.00-1.37	.10-.15	.64- .98	.22-.34	.01- .59
Current	Whorl 3	1.08-1.31	.07-.13	.72- .89	.23-.41	.26- .63
2 years	Whorl 2	0.98-1.19	.04-.11	.55- .92	.36-.70	.84-1.72
2 years	Whorl 3	0.97-1.32	.05-.11	.59- .92	.16-.27	.99-1.70
3 years	Whorl 3	0.94-1.11	.08-.11	.54- .89	.18-.31	.90-2.27

[1]Whorls are counted from the top of the crown.
[2]Ash residue (for details cf. text).

TABLE 2. Statistical data for relationship between tree height and nutrient concentration in needles.

Needle Age	Location of Shoot	Linear correlation coefficients					Regression coefficients				
		N	P	K	Ca	A	N	P	K	Ca	A
Current	Terminal	.785	.731	.679	.255	.313	.043	.007	.059	-----	-----
Current	Whorl 1	.579	.836	.774	—.185	.729	.022	.005	.038	-----	.052
Current	Whorl 2	.602	.796	.691	—.214	.385	.022	.004	.023	-----	-----
Current	Whorl 3	.185	—.097	.578	.673	.607	-----	-----	-----	.011	.026
2 years	Whorl 2	.401	.473	.773	.386	.507	-----	-----	.027	-----	-----
2 years	Whorl 3	.386	.384	.703	.248	.488	-----	-----	.023	-----	-----
3 years	Whorl 3	—.259	—.157	.522	.537	.576	-----	-----	-----	-----	-----

(For p = .01, r = .765; for p = .05, r = .632.)

is concerned, needles from the terminal shoot provide the greatest degree of differentiation between trees of different height and that, where comparisons are possible, this differentiation becomes less marked as one progresses down the crown or samples older needles.

The interpretation of relationships based on simple correlation coefficients is complicated by the possibility of interrelationships between individual nutrients. It is therefore of some interest to consider these relationships in terms of multiple regressions of tree height on nutrient concentration. If all nutrient factors are concerned, we can calculate in each case a multiple regression equation of the form:

$$Y = b_1N + b_2P + b_3K + b_4Ca + b_5A + k$$

where Y is the estimated tree height (ft.), and N, P, etc. are N, percent dry weight; P, percent dry weight, etc. Data for the partial regression coefficients b_1, b_2, b_3, etc., and the constants k are given in Table 3, together with the corresponding multiple regression coefficients, R (representing the correlation between actual and estimated heights) and the standard errors of the estimates, S.E.

According to these data it would seem that tree height can be related to the mineral composition of any of the needles sampled from the upper part of the crown, but that the accuracy of the estimates is greatest in the terminal needles and decreases as one descends the crown. Between the various needle samples, however, the nature of the function varies considerably; e.g. for the current needles, the coefficient for the N factor shows a progressive change from a positive value in the terminal shoots to a similar but negative value in Whorl 3.

TABLE 3. Data for multiple regressions of tree height on nutrient concentration in needles.

Needle Age	Location of Shoot	Partial regression coefficients b_1(N)	b_2(P)	b_3(K)	b_4(Ca)	b_5(A)	k	R	S.E. (ft.)
Current	Terminal	14.0	−36.4	8.4	0.6	5.7	−16.6	.972	1.12
Current	Whorl 1	11.4	−47.0	16.8	0.5	4.4	−15.1	.942	1.59
Current	Whorl 2	− 7.6	125.5	15.7	− 0.2	4.6	−12.0	.928	1.76
Current	Whorl 3	−14.9	28.9	33.1	−32.2	9.8	−15.4	.915	1.91
2 years	Whorl 2	14.5	4.9	22.5	−11.7	5.5	−24.6	.921	1.84
2 years	Whorl 3	2.6	61.4	16.5	−19.9	5.3	−14.6	.813	2.76
3 years	Whorl 3	−34.2	−16.8	15.4	4.2	3.3	29.0	.880	2.25

(For $p = .01$, $R = .917$; for $p = .05$, $R = .811$.)

TABLE 4. Test for significance of partial regression coefficients.

Needle Age	Location of Shoot	Values for "t" b_1(N)	b_2(P)	b_3(K)	b_4(Ca)	b_5(A)
Current	Terminal	3.73	1.14	3.00	.06	2.17
Current	Whorl 1	1.67	.52	2.39	.02	.84
Current	Whorl 2	.82	2.57	2.21	.01	1.20
Current	Whorl 3	1.39	.47	1.78	1.74	1.68
2 years	Whorl 2	.64	.12	3.10	1.17	1.45
2 years	Whorl 3	.26	1.03	1.62	.65	.87
3 years	Whorl 3	1.58	.20	2.26	.10	.70

(For $p > .05$, $t > 2.78$.)

These regression equations of course give no direct information as to the significance of the contributions made by the individual nutrient factors. Such information may be obtained by calculating the standard error for each partial regression coefficient and testing for significance by applying the "t" test. The results of these tests are summarized in Table 4.

Despite the suggestions of significant multiple regressions of tree height on nutrient concentration in all needle samples (Table 3) it would appear from these "t" tests that in only two cases are the individual nutrients associated with significant (5%) partial regression coefficients viz. N and K in the terminal needles and K only in the two year old needles from Whorl 2. Evidently the existence of significant simple correlations between tree height and the concentration of a particular nutrient does not necessarily imply a significant contribution of that nutrient to the multiple regression. In many cases this must be due to significant interrelationships between individual nutrients e.g. in the terminal needles, P is significantly correlated with tree height but this is apparently a reflection of the K relationship since K and P are significantly correlated with each other ($r = .835$) and only K makes a significant contribution to the regression. It is also evident that a significant multiple correlation, as for example in the case of the needles from Whorl 1 (cf. Table 3), does not necessarily imply the existence of significant contributions from any of the individual nutrients. Again it is possible that the overall relationship between tree height and needle composition is influenced by interrelationships between individual nutrients.

In the case of the needles from the terminal shoots, the regression analysis can be modified to exclude all factors other than N and K since only these two nutrients are associated with significant partial regression coefficients. The new regression equation is:

$$Y = 11.79\,N + 5.70\,K - 10.18$$

yielding a highly significant multiple correlation coefficient of $R = .919$ and a standard error of ± 1.41 feet.

The relationship between needle composition and dry weight production. Data for the total dry weights of the above ground parts of each tree are given below together with the corresponding tree heights:

Tree ht. (ft.)	4.3	3.5	6.0	7.0	8.5	9.5	10.0	11.0	12.5	14.0
Dry wt. (kg.)	.54	.38	.71	.73	1.59	2.41	2.56	4.48	7.56	6.95

Analysis of these data reveals a highly significant linear component of the relationship between height and dry weight ($r = 0.929$) and it might be expected therefore that dry weight can also be related to needle composition. This is confirmed, for the current needles at least, by the multiple regressions, data for which are presented in Table 5.

Though still significant, the multiple correlation coefficients for dry weight are a little lower than those for tree height (cf. Table 3) and the estimates, therefore, correspondingly less precise. The partial regression coefficients for individual nutrients also differ from those relating to height but not so greatly as to suggest a fundamentally different kind of relationship. This view is supported by the "t" values for the various regression coefficients which again indicate the significance of the contributions made by the N and K factors in the terminal needles. There is also some suggestion that the same two nutrient factors are mainly concerned in the regression based on the needles from Whorl 1, a situation which is much less apparent from the corresponding height data (cf. Table 4).

Discussion and Conclusions

One of the main factors determining the choice of material for foliar analysis is the degree of differentiation obtained between plants of different growth vigor. Insofar as the deductions based on the present experimental material are valid, it would appear

TABLE 5. Data for multiple regression of above ground dry weight on nutrient concentration in current needles.

	N		P		K		Ca		A		
	b_1	t	b_2	t	b_3	t	b_4	t	b_5	t	R
Terminal	16.01	3.95	—73.1	2.13	8.6	2.85	— 7.9	.76	5.5	1.96	.954
Whorl 1	17.0	2.46	—88.4	.89	18.8	2.65	13.9	.63	1.2	.22	.916
Whorl 2	— 6.1	.51	90.6	1.43	12.5	1.36	12.9	.60	4.3	.87	.820
Whorl 3	— 7.2	.55	—41.3	.55	7.9	.35	36.8	1.64	4.5	.64	.815

b_1, b_2, etc. = partial regression coefficients
t = corresponding "t" value
R = multiple correlation coefficient

that the most suitable material is provided by needles from the terminal shoot. In practice of course this method of sampling is not possible if normal tree growth is to be maintained and under such circumstances, sampling is then best restricted to the current needles from the topmost lateral shoot. Current needles lower down the crown, or older needles, provide a much poorer basis for differentiation whilst samples representative of the whole crown may lead to completely different conclusions. This may be one of the reasons why previous investigators (e.g. Aaltonen, 1950) have been led to reject foliar analysis as a reliable guide to nutrient availability.

As regards the subsequent analysis of the relationship between tree growth and needle composition it must be emphasized that the interpretation of the results in terms of nutrient deficiencies rests on a number of assumptions, direct proof of which has not been put forward in this investigation. Basic to this particular approach is the assumption that the selection of trees of varying height in an even-aged plantation constitutes a valid sample. Besides heterogeneity in soil conditions, there are a number of other possible factors (genetic, planting stock vigor, treatment during planting, etc.) which would ultimately result in uneven growth and there is therefore no direct proof of a causal relationship between nutrient supply and growth, no matter how closely growth is related to the nutrient status of the foliage. The argument has been presented that a significant linear correlation between tree growth and the concentration of a particular nutrient in the needles implies a deficiency in that nutrient insofar as an increased concentration of that nutrient is then associated with increased growth. In practice, however, this assumes that increased concentrations in the needles can be brought about by increased supply via the soil and though previous investigations have shown this to be generally true under conditions of a deficiency of one nutrient (Mitchell, 1939; Mitchell and Chandler, 1939; Heiberg and White, 1951) the interpretation becomes rather more complicated when more than one nutrient is related to growth as in the present case with needles from the terminal shoots. Under these circumstances and because of possible interrelationships between nutrients, it seems logical to extend the analysis of the results to multiple regressions based on a number of nutrients. This approach implies that height is a function of nutrient status, a situation which can only be demonstrated by actual fertilizer trials in the field. It must also be emphasized that because of the small number of samples and the relatively large number of variables included in the regression, the statistical analysis should not be interpreted too strictly, especially when many of the variables are interrelated with each other. Nevertheless the fact that, in all cases, tree height can be significantly related to needle composition and that similar results have

been obtained elsewhere with another species using a much larger sample (Leyton, 1955) suggests that the observed relationships deserve a certain amount of attention. It has been shown for example that the terminal needles provide the closest agreement between actual and estimated heights (Table 3) and that the precision of the estimates tends to fall progressively as one samples lower down the crown. Within the limitations set by the investigation, this would confirm the advisability of sampling as near to the terminal shoot as possible. It would also appear in the case of the terminal shoot at least, that only nitrogen and potassium make significant contributions to the regression, and that the significant linear correlation between height and phosphate concentration result from the interrelationship of this nutrient with potassium. In the absence of actual fertilizer responses, the precise significance of these findings cannot be fully explained but the argument is tentatively put forward that the height growth of the trees is limited only by nitrogen and potassium insofar as only increased concentrations of these nutrients would be equivalent to increased growth. It must be admitted of course that the analyses give no indication as to how the concentration of these other nutrients will be affected by the addition of either nitrogen or potassium; theoretically, however, the relationship with height growth is independent of the concentration of other nutrients, provided that these remain within the range encountered in the present investigation; on this basis, therefore, only the interrelationship between nitrogen and potassium would appear to be involved. Experience with the growth of pines on comparable sites would confirm the presence of nitrogen deficiencies (Leyton, 1954) but as yet no evidence has been obtained for the presence of potassium deficiencies in these soils.

Since the total dry weight of the above ground parts of the trees was found to be closely related to height growth it was not surprising to find that dry weight could also be related to the nutrient composition of the needles with more or less similar results. This would suggest that, under these circumstances, height is a reasonably fundamental measure of growth.

Summary

Significant linear correlations have been established between the height growth of Scots pine growing in an even-aged plantation on heathland, and the concentration of various nutrients in needles of different age sampled from various parts of the crown; in the case of needles from the terminal shoots, nitrogen, phosphorus and potassium were all significantly related to growth.

The degree of differentiation between trees of different height, in terms of nutrient concentration in the current needles, was greatest in the terminal shoots and decreased progressively down the crown; with the exception of potassium, no differentiation was obtainable with older needles. It is suggested that current needles from as near the terminal shoot as possible provide the best material for foliar analysis.

For all needle samples, tree height can be significantly related to needle composition (N, P, K, Ca and other ash constituents) by means of multiple regression equations; the best estimate, with needles from the terminal shoot, yields a multiple correlation coefficient of 0.972 and a standard error of ± 1.12 feet. Tests on the partial regression coefficients for each nutrient suggest that, in the case of the terminal needles at least, only nitrogen and potassium make significant contributions to the regression; for these needles the function 11.79 N (% D.wt.) + 5.70 K (% D.wt.) — 10.18 provides an estimate of tree height with a standard error of ± 1.41 feet.

It is tentatively suggested from these results that the growth of the pines is limited by deficiencies in nitrogen and potassium insofar as increased concentrations of

these nutrients in the needles, independent of the concentrations of other nutrients within the range encountered, are associated with increased height growth.

A significant linear component has been established for the relationship between height and the total dry weight of the above ground parts of the trees. These dry weights can also be expressed in terms of regressions on nutrient concentration in the needles and the resulting functions more or less agree with those for tree height.

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A Stain Technique for Diagnosing Blister Rust in Cankers on White Pine

BY
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IN THE RESEARCH and control program for white pine blister rust, it is frequently necessary to diagnose cankers that resemble blister rust cankers but do not have the typical symptoms necessary for an exact identification. If such cankers occur in areas where blister rust has not been reported previously, a correct diagnosis is essential.

For some years, diagnoses of this type have been made by the writer from specimens collected in the eastern United States (*Pinus strobus* L.). A staining technique has been devised that is particularly well adapted to this work, because it is rapid and gives satisfactory differential staining of host and fungus.

Stains Considered

Several stains that combine an acid and a basic dye have been used to differentiate between mycelium of the rust fungus and host tissue. Colley described in detail the use of safranin and lichtgruen in staining microtome sections cut with a freezing microtome (1917) or prepared by the paraffin or celloidin method (1918). With these dyes, sections can be stained rapidly, but, for satisfactory differentiation, the process must be watched carefully to obtain the proper balance between the stains.

A staining technique with orseillin and aniline blue, described by Strasburger (1923), was used successfully by Hutchinson (1935) for determining the presence of fungus mycelium in pine affected by the disease known as Woodgate rust. This technique, slightly revised, has been used by the writer for staining sections of white pine blister rust cankers that were cut with the freezing microtome. The stain gave excellent results in detecting the mycelium of the fungus, particularly in newly infected twigs and needles, as well as in the wood at the outermost margins of the cankers. However, the red orseillin dye is slow acting; it requires a staining period of 12 hours or overnight. This is followed by a half-hour staining period with the aniline blue. Although the results of the stain are more dependable than the safranin-lichtgruen combination, the longer period necessary for staining is undesirable when rapid diagnosis is required.

Pianeze IIIb stain (1896, p. 58) has been used extensively in pathological studies to detect fungus mycelium in all kinds of host tissue. The stain fades slowly in the tracheids of the pine and sometimes has proved undesirable for permanent mounts. However, for rapid diagnosis of cankers it may be used successfully. Vaughan (1914) made some changes in technique. To diagnose blister rust in cankers of white pine, the writer has made changes in both stain formula and technique.

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The New Technique

A killing solution is not used. From the upper margin of the canker or from any portion of a twig or branch that resembles an area of infection by the blister rust fungus, cut a block of bark and wood of a size adapted to sectioning on a freezing microtome. The size of the block also depends upon the diameter of the part of the host that is infected. For a recent infection on a small twig ¼ inch or less in diameter, the block to be sectioned should be a cross section of the twig about ¼ inch long. From twigs of larger diameter and from branch or stem cankers, the block should be about ¼ inch on a side and should include the bark and the wood or one or two annual rings. If the specimen has dried out and the bark separates readily from the wood, the bark and the wood should be cut separately.

Boil the block in water until most of the resin and air is removed. Then submerge it in a 10-percent water solution of gum arabic for 5 to 10 minutes. Mount the block in gum arabic solution and freeze the block on the disk of a freezing microtome. Cut radial sections 20–25μ thick, or even thicker, depending on the character of the specimen. Firm smooth sections are needed in order to retain mycelium and affected host cells.

From cankers on stems or branches ½ inch or more in diameter, mount a larger block, boiled in water, directly on a sliding microtome and section it radially. In either case, use a brush to remove the sections from the knife and place them in water in a bevel-ground Syracuse watch glass. Draw off the water and add the stain.

The revised formula for the stain is as follows:

Malachite green	0.50	g.
Acid fuchsin	0.10	g.
Martius gelb	0.01	g.
Water, distilled	150.0	cc.
Alcohol, 95 percent	50.0	cc.
Glacial acetic acid	1.0	cc.

The addition of the glacial acetic acid to the stain solution (instead of drawing off the stain and rinsing the sections in acid alcohol as recommended by Vaughan (1914)) intensifies the the staining of the sections, making the red stain more vivid and the green slightly more lasting.

Stain the sections for 1 hour, draw off the stain solution, and rinse the sections twice in 95 percent alcohol. Then rinse them once in absolute alcohol and clear them in clove oil. For prompt examination under the microscope, clear them for 10 to 15 minutes and mount them in clove oil on a slide. For permanent mounts, clear the sections for 6 hours or even overnight, rinse them thoroughly in xylol, and mount them in balsam or any other suitable medium.

Diagnostic Characteristics

In a radial section, the mycelium, medullary ray cells of the host, and the resin-duct parenchyma cells stain red; the tracheids stain green. The blister rust fungus can be distinguished from other canker-producing or secondary fungi because the mycelium of the blister rust fungus has the following characteristics: (1) wider hyphae, (2) intercellular hyphae among the medullary rays distinctly separating the ray cells, and (3) conspicuous haustoria forming in the bark cells of newly infected twigs and particularly in the ray cells of bark and wood in older infected areas. These characteristics were well illustrated by Colley (1918, plate 53).

The hyphae of the blister rust fungus are uniformly wider than those of other fungi that invade pine bark. With the revised Pianeze IIIb stain, they consistently stain light bluish-red in the advancing tips, bright red in well-developed hyphae, and purplish in older portions. The small nuclei are conspicuous, staining dark red, almost black. Although most of the mycelium stains the same tint of red as the medullary ray cells, its intercellular position and the haustoria are easily distinguished.

The haustoria are formed as branches of the intercellular hyphae, becoming con-

stricted as they pass through the cell walls, then expanding to the ordinary size of the hyphae. They may be straight or curved, usually extending toward or around the nucleus of the host cells. In heavily infected wood, hyphae penetrate between the walls of the tracheids, and short haustoria may pass through the walls into the tracheids, but they do not advance farther.

Hyphae of other canker-producing fungi also stain red and may invade the medullary ray cells and the tracheids. They are intracellular, narrow, and branched, without haustoria, and they pass from one cell to another through the bordered pits.

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Volume Table Construction

The volume-basal area line. A study in forest mensuration. By F. C. Hummel. Forestry Commission Bull. 24. 1955. 84 pp. Available from Her Majesty's Stationery Office, London. 9 shillings.

REVIEW by Stephen H. Spurr

University of Michigan

This British report is a detailed statistical study that lets the reader know exactly what was done and how well an end purpose was accomplished. The title is misleading, referring to the fact that a linear relationship (the volume line) was found to exist between volume and basal area in both the construction of standard volume table construction that the bulletin is concerned.

The first three chapters deal with the construction of standard volume tables by regression analysis or graphical short-cuts that take into account linear relationships where they occur (as the volume-basal area one) and yet allow for curvilinear analysis when that proves necessary. This part details the methods by which the recent British volume tables were constructed, and they are sound, whether used for species tables or composite tables.

The second part of Hummel's work is concerned with the development of composite local volume tables (termed Tariff tables in Britain). Using large numbers of data obtained from several different conifers, Hummel demonstrates that, in any given even-aged stand, the form factor is not constant as assumed by Gevorkiantz and Olsen in their cubic-foot solution. Expressed another way, the volume-basal area regression does not pass through the origin. Rather, the tree has zero volume when the basal area is 0.03 square feet and the regression solution passed through that point (z'). Hummel demonstrates that this constant holds for a wide range of species and heights so that composite local volume tables may be based upon it. With a sample of about eight trees, a satisfactory local volume table can be chosen that will fit an even-aged stand.

The British tables may well be useful in American practice. At any rate, they should serve to provide ideas both as to techniques and as to presentation.

Stem Taper of Trembling Aspen

BY

HENRY A. STOEHR

STEM TAPER varies between stands and between trees in the same stand. Foresters generally agree that trees of the same species differ in stem form primarily because of external factors. Metzger believed that wood formation in tree stems is governed by the requirements of the tree for mechanical strength in order to counteract the pressure of the wind against its crown. Hohenadl found that dominant trees showed a greater increment in the lower part of the stem as a consequence of the necessity of supporting the weight of the portion of the tree above the base. Several foresters have reported a decrease in taper and consequent improvement in stem form as a result of stand treatment. Thinning was found to result in an increase in diameter growth in the upper part of the stem (Behre, 1929; Bickerstaff, 1946). Trees left after selective logging, however, seem to grow proportionately more in diameter at the base than higher up the tree (Krauch, 1913; Behre, 1929; Meyer, 1931; Schumacher, 1932). Release cutting in the understory of yellow-poplar resulted in greater diameter growth at the base of the dominant trees (Holsoe, 1951; Lange, 1951). Pruning resulted in increased diameter growth in the upper part of the tree stem, with a subsequent improvement in form (Young and Kramer, 1952).

This study is an evaluation of the external factors that affect stem form in pure, unmanaged, even-aged stands of trembling aspen (*Populus tremuloides*, Michx.). This species was chosen because of its wide distribution and increasing economic importance in the Lake States region.

The study was confined to a contiguous area in Iosco and Alcona counties, Michigan. These two counties comprise most of the Tawas Ranger District of the Huron National Forest. Alcona County has much more extensive stands of trembling aspen than does Iosco County. The topography is more rolling and the soil conditions are more diverse. Aspen is found in Iosco County chiefly in the northern part in the vicinity of the Au Sable River, adjacent to Alcona County.

Methods

Sixty temporary sample plots were established in even-aged stands of trembling aspen ranging from eighteen to fifty years old. Stands were located previous to the actual field work on cover-type maps prepared from aerial photographs by the

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The author was formerly Assistant Professor at Michigan State College, and is now Associate Professor of Forestry at the University of Georgia. This article is based upon a doctoral thesis submitted to the University of Michigan, and prepared under the supervision of Prof. John Carow. Prof. F. X. Schumacher of Duke University also helped in planning the study.

United States Forest Service. These sample plots were located no closer than one-fourth mile apart in order to minimize duplication of any given combination of stand conditions as to site, age or density.

In the field, each plot was located so that the distribution of trees in it would be as uniform as possible. Extremely poor sites bordering the sand plains were avoided because the trees on such areas are deformed and show high incidence of disease. Each plot was rectangular in shape. Its boundaries were laid out with staff compass and metallic tape and marked with string. Plot size varied from .01-acre for dense, young stands to 0.1-acre for older, low-density stands, in order to include at least fifty trees on each plot.

The diameters of all living trees on each plot were measured with tree calipers at breast height and tallied by 1-inch diameter and crown classes. Four crown classes were used: dominant, codominant, intermediate and suppressed.[1] Eight sample trees, two for each crown class, were chosen at random on each plot, were felled and measured. The stem of each tree was marked at intervals equal to one-tenth of the total height, for the entire length of the tree. Diameters outside bark were measured at these ten points with the tree calipers, and the thickness of the bark was determined with the Swedish bark gauge. Annual rings were counted.

Analysis of Data

The d.b.h.-form factor[2] was used as an expression of tree stem form or taper because of its simplicity and because the entire stem of the tree is taken into consideration (Bruce and Schumacher, 1950). The volume of the entire stem inside bark was computed by the graphic method (Spurr, 1952), as was the corresponding cylinder volume for each tree. The plot form factor was expressed as the average form factor for the eight sample trees.

The number of trees on each plot by crown class and their basal area in square feet were expressed on a per acre basis. The d.b.h. of the average tree was computed from average basal area. Stand age and height were based on dominant and codominant trees. Site index was interpolated from the site index chart (Brown and Gevorkiantz, 1934) for age fifty years. Stand density index in percent of normal stocking was interpolated from a stand density index chart (Figure 1).[3]

Findings

It was found that the d.b.h.-form factor differs not only from stand to stand, but between trees of the same stand as well. The average form factor for dominant trees was 47.9, the average for codominant trees was 49.4, for intermediate trees it was 49.9 and for suppressed trees it was 57.6. The average for all trees was 51.2. Whether these differences are significant or not, and if so, to which of the variables they can be attributed was tested from three aspects:

1. Effect of crown class, or position of the tree's crown relative to the forest canopy, on form factor within the stand.
2. Effect of stand conditions on stand form factor, between stands.
3. Effect of stand conditions on form

[1]Forestry Terminology, Society of American Foresters, 1950.

[2]The d.b.h.-form factor is the ratio of the entire stem volume and the volume of the cylinder whose diameter is equal to d.b.h. inside bark and whose length is the total height of the tree.

[3]Values for the construction of the stand density index chart were taken from the normal yield table for trembling aspen, and a straight-line curve was fitted to the coordinate points plotted on log cross-section paper by the method of least squares. The regression equation by least squares is: $\text{Log } N = -1.515 \log D + 3.953$ in which N = number of trees per acre and D = average d.b.h. The number of trees for stands below and above normal stocking were computed at ten percent and twenty percent intervals respectively. This resulted in a series of parallel lines (Figure 1).

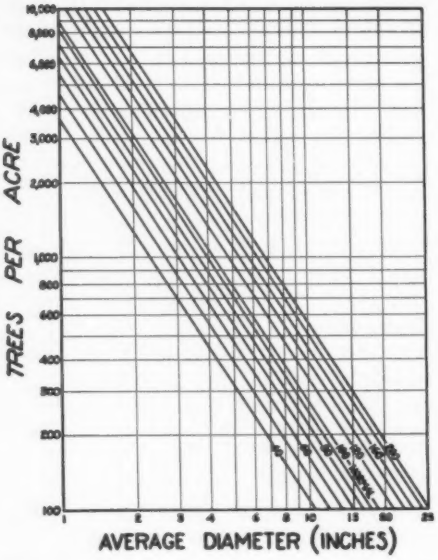

FIGURE 1. Stand density index graph for trembling aspen.

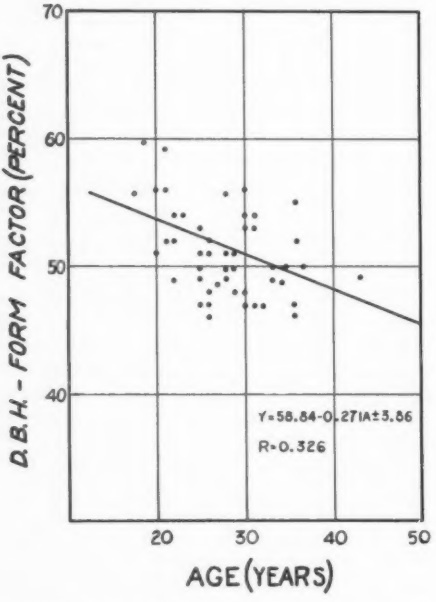

FIGURE 2. Regression of age on stand form factor for trembling aspen.

factor for each crown class, between stands.

The overall effect of stand conditions and crown classes on form factor was tested by means of analysis of the variance for all 480 sample trees. Differences in stand form factor between plots due to the combined effect of age, site and stand density were found to be highly significant (at the 1-percent level) as are differences between the four crown classes. The lack of significance of the interaction found between stands and crown classes is due to the progressive trend of the average form factors between crown classes, increasing from dominant through the suppressed classes.

Effect of crown class within the stand. Analyses of differences between means for each of the four crown classes were made by using the "t-test." There was no significant difference between the average form factors for the first three crown classes, dominant, codominant and intermediate trees, but that the average form factor for the suppressed trees was greater than the other three crown classes to a highly significant degree.

Effect of stand conditions on stand form factor. The effect of the three stand factors—age, site and stand density—can be shown by the following regression equation:

$$Y = 77.908 - 0.308X_1 - 0.255X_2 - 0.026X_3$$

in which Y is the stand form factor, X_1 is age of stand in years, X_2 is site index in feet at 50 years, and X_3 is stand density index expressed as a percent of normal density. The standard error of estimate is ± 3.38 form factor units.

The standard deviations for each regression coefficient were obtained by solving for the Gauss multipliers so that the regression equation can be written more fully:

$$Y = (77.908 \pm 0.436) - (0.308 \pm 0.077)X_1 - (0.255 \pm 0.067)X_2 - (0.026 \pm 0.016)X_3 \pm 3.376$$

Any regression coefficient that is at

least three times greater than its own standard deviation is regarded as significant (Fisher, 1944).

It was found that age, site, and stand density, taken together, are highly significant (1 percent level), as is age and site taken together, and site alone. Age alone was significant (5 percent level) and stand density alone was not significant. It is evident that site quality is the limiting factor in the determination of form factor for the stand as a whole. Moreover, as site index increases, the stand form factor decreases. The correlation between age and stand form factor is shown graphically in Figure 2, and between site index and stand form factor in Figure 3.

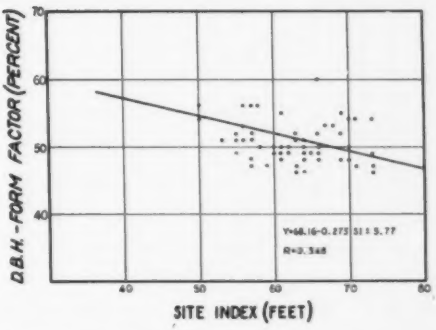

FIGURE 3. Regression of site index on stand form factor for trembling aspen.

Effect of stand conditions, each crown class. The effect of each of the stand factors—age, site, and stand density—on the form factor for each crown class can be shown by the following regression equations:

Dominant trees:

$$Y = 61.002 - 0.082X_1 - 0.205X_2 + 0.022X_3 \pm 3.113$$

Codominant trees:

$$Y = 63.949 - 0.131X_1 - 0.146X_2 - 0.020X_3 \pm 3.362$$

Intermediate trees:

$$Y = 66.550 - 0.003X_1 - 0.289X_2 + 0.015X_3 \pm 3.450$$

Suppressed trees:

$$Y = 118.322 - 0.729X_1 - 0.539X_2 - 0.080X_3 \pm 9.225$$

The effect of the various stand factors differs considerably in significance between crown classes when analyzed by analysis of variance. The levels of significance for stand variables do not apply to each crown class separately in the same way as they did to the entire stand, or all crown classes combined. For example, the form factor for trees in the dominant and codominant crown classes are not significantly affected by age, site, or stand density. The form factor for trees in the intermediate classes, however, shows a significant effect for age and site combined, whether or not stand density is included, and high significance for site index. The form factor for the suppressed class is highly significantly affected by all stand conditions with the exception of stand density. Form factors for the dominant and codominant trees are not significantly affected by changes in stand conditions, although dominant trees do seem to show some response to changes or difference in site quality. It is evident that site quality is the most uniform influence upon form factor. Only in the codominant class did it lack significant effect. Stand density, on the other hand, lacked a significant effect on all four crown classes.

While the form factor used in this study does not lend itself to direct measurement in the field and would have to be replaced by a measure such as form quotient that is more easily made, the results with trembling aspen indicate that the measurements of average form for given stands can best be made on codominant trees. The form factor for codominant trees was found to be least affected by changes in stand conditions. Also, as natural stands increase in age, the percentage distribution of trees in the codominant classes increases (Figure 4). Therefore, the volumes for stands thirty years and over will be made up predominantly by codominant trees.

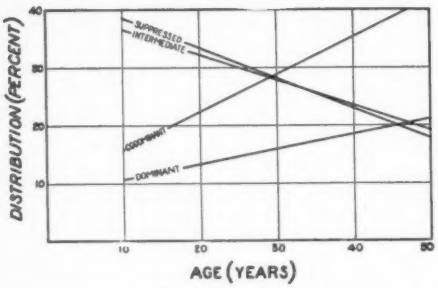

FIGURE 4. Effect of age on distribution of crown classes for trembling aspen.

Summary

Stem analyses were made on 480 aspen trees in 60 temporary sample plots on the Huron National Forest in Michigan. The purpose of the study was to relate the variation of d.b.h.-form factor for pure, unmanaged, even-aged stands of aspen (*Populus tremuloides*, Michx.) to age, density, site quality and crown class.

It was found that the stand variables, age, site and density, acting together, resulted in a highly significant difference in the average form factor between stands. No one or any combination of two variables increased in magnitude, the average the three of them acting in combination. Individually, site index showed the greatest effect, age less effect, and stand density no significant effect. As these three variables increased in magnitude, the average form factor decreased.

The difference in form factor between dominant, co-dominant, and intermediate trees was not significant, while the form factor for suppressed trees was significantly higher than the other three crown classes. The codominant trees were affected the least by the variation in stand conditions, while the suppressed trees were affected the most.

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Evaluation of Three Thinnings at Star Lake

BY

F. G. WILSON

THIS MATCHED PAIR of one-acre plots of red pine (*Pinus resinosa Ait.*), each with a one chain wide isolation strip, was established in the spring of 1943 when this 6- by 6-foot plantation was 30 years old and the trees were 32 years old from seed. The trees in each plot were numbered and measurements were taken as outlined by the Lake States Forest Experiment Station, which files the data taken at each thinning. Before the first thinning, the plots differed by 57 trees and two square feet of basal area. Thinning has been generally from below, but has taken larger trees with coarse branches or showing defects. The record to date is summarized in Table 1.

Control of Stand Density

While the first thinning was endorsed by many foresters as "about right", some held that the residual basal area of 140 square feet was too high. Efforts to check the latter opinion led the writer (1946) to the formula based on height:

$$n = \frac{43{,}560}{(hf)^2}$$

Where n is the number of trees per acre, h is the height of the stand in feet, and f is any fraction or percent of height. References then made to normality are retracted; the formula is abstract and provides a diagonal grid (Fig. 1) on which the course of an even-aged plot or yield table can be plotted and evaluated. Since the pattern of spacing in a stand changes with each thinning, nothing would be gained by using other than the commonly-assumed square spacing.

The position of the upper portion of the curve for any data depends on the density at which the stand was established. The curves for the many yield tables which the writer has plotted, whether for managed or natural stands, all show a downward trend toward the end of the rotation. This is natural because crowns continue to spread while the rate of height growth declines. For the same species, poorer sites carry fewer trees for height than good sites. The same is true for intolerant species as compared to tolerants unless there is marked difference in thinning schedules on which yield tables are based. For sites with comparable height at fifty years, the curves for spruce in Denmark may fall below those for heaviest thinning of pine in Germany.

When it was found that the first thinning at Star Lake left a stand density of 20.6 percent of height of dominants, it was decided to follow this line to the nearest ten trees per acre for several thinnings and learn what happens to other values. The same number of trees is left on each

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The author, former Superintendent of Cooperative Forestry, Wisconsin Conservation Department, has conducted the three thinnings, the last during his year as Assistant Professor at Michigan College of Mining and Technology.

TABLE 1 – Star Lake Plantation – Summary Table – Red Pine – Permanent Sample Plots – One Acre.

	Height		D. B. H.		No. of Trees	Stand Density	Basal Area	Bole Area	Peeled Vol.	Cords Rough	Saw Timber
	Dom.	Ave.	Range	Ave.		Per Cent(1)	Sq. Ft.	M. Sq. Ft.	Cu. Ft.		Bd. Ft.(2)
	Feet		Inches								
CHECK PLOT											
Age 30	42	40	1.0-9.2	6.0	893	16.6	172	36.7	2,842	35.4	1,770
5 year increment	+7			+.4			+22		+741	+9.5	+2,390
Age 35, live trees	49	46	2.1-9.5	6.4	873	14.4	194	44.1	3,583	44.9	4,160
Mortality			*1.0-4.4*	*3.1*	−20		−1		−6	−0	−0
6 year increment	+6			+.3			+11		+1,029	+12.6	+5,030
Age 41, live trees	55	52	3.4-10.5	6.7	844	13.1	205	50.8	4,612	57.5	9,190
Mortality			*2.2-8.5*	*4.2*	− 29		−3		−50	−.4	−60
THINNED PLOT											
Age 30	42	40	1.8-9.9	6.2	836	17.2	174	35.5	2,885	35.9	2,770
Cut, 1st Thinning			*1.8-9.0*	*5.0*	−256		−34		−539	−5.9	−120
1st residual	42	41	3.0-9.9	6.6	580	20.6	140	26.8	2,346	30.0	2,650
5 year increment	+7			+5			+22		+771	+9.0	+3,330
Age 35	49	47.5	3.1-10.7	7.1	580	17.7	162	33.5	3,117	39.0	5,980
Cut, 2nd Thinning			*3.1-8.8*	*6.0*	−150		−30		−538	−6.7	−450
2nd residual	49	48.5	5.0-10.7	7.5	430	20.6	132	26.8	2,579	32.3	5,530
6 year increment	+8			+.6			+21.5		+1,003	+12.6	+6,040
Age 41	57	56.5	5.1-11.2	8.1	429	17.7	153.5	33.8	3,582	44.9	11,570
Cut, 3rd Thinning			*5.1-10.5*	*7.4*	−109		−32.5		−738	−9.3	−1,870
3rd Residual	57	57	6.0-11.2	8.3	320	20.5	121	26.1	2,844	35.6	9,700
Three cuts plus last residual.									4,659	57.5	12,140

(1) Spacing in per cent of height of dominants.
(2) Decimal C rule, in trees 7" and over.

square chain as an aid to uniform distribution over the acre. It was further decided to time thinnings with each added seven to eight feet of height growth. A British publication (Anon., 1945) advised that thinnings should be repeated with not more than ten feet of height growth. These two rules will control stand density until the height of 65 feet at 50 years from seed is reached, the thinned plot having three times fallen on this top line of the site index graph for red pine in the Lake States. (Eyre et al., 1948) Thereafter the curve defining the residual stand should turn downward.

The courses of this plot, with three thinnings and two intervals of growth, and of the untreated check plot are shown in Fig. 1. Current height growth of dominants for the latter fell behind that for the thinned plot after spacing became closer than one-seventh of height. To Fig. 1 has been added the curve defining residual stands for the heaviest or accretion thinning (*Lichtung*) for Scotch pine on Site I, also site 65 feet at 50 years, from the yield tables by Wiedemann (1949). Also shown is the second thinning at ten years from the table "Composite Thinning Regime" for Monterey pine (*Pinus radiata* D. Don) on site I in South Africa by Craib (1939). This comparison of similar degrees of thinning of three hard pines on three continents is possible because, as the writer stated when first submitting the formula: *Height has the virtue of combining the components of age and site in one measurement.*

Reaction of Basal Area

With three thinnings to the same density in terms of height, the course of the red pine thinned plot continues to approach the Wiedemann curve as to number of trees. But with fewer trees per acre, it still has more basal area (Fig. 2) because of the greater but decreasing difference in average d.b.h. for trees of the same age and height,

(Fig. 3). With wider initial spacing and a prolonged period of high live-crown ratio, the red pine trees had developed excessive taper, which, with negligible loss of trees after reaching breast height, resulted in an inflated basal area value at the time of the first thinning.

In plantations of 6 x 6 feet or wider, a high basal area, even when supported by a marked slowing down of diameter growth *at breast height*, is no indication that the plantation is stagnating and must be thinned. What is happening is both normal and desirable: The trees are correcting their form for height and greater stand density, as evidenced by wider annual rings higher on the stem. Upper diameters govern utilization, which explains the high increments in cords or board feet while diameter growth at breast height was at the low rate of only 20 rings to the last radial inch. Using the German system of ratios in the same unit of measure, the height/diameter ratio for the average tree in the Star Lake check plot has risen from 74:1 to 93:1 during the age period when such ratios derived from German yield tables are declining because excessive taper never developed, and because breast height is proportionately lower as total height increases. For the residual stands the h/d ratio has risen from 74:1 to 82:1. When these trees have fully corrected their form for the maintained density the rate of diameter growth at breast height will increase, perhaps retarding the decline in residual basal area.

Using Bole Area as a Check

When the second thinning revealed a decrease of residual basal area, some concern was felt that thinning to same density in percent of height might deplete growing stock. Bole area proposed by Lexen (1943) was tried in the crude form of dividing the product of height in feet times d.b.h. in inches for the average tree by 7, an average figure suggested by Lexen for ponderosa pine. Following the third thinning, bole area factors for the average tree at the time of each thinning were computed by stem analysis of cut trees. Total bole areas for the check plot at the time of the second and third measurements are less valid because the trees have less taper and the range in d.b.h. is wider, so these values are not used in Fig. 4. Yet the demand on a square foot of ground to nourish more than a square foot of stem cambium appears excessive.

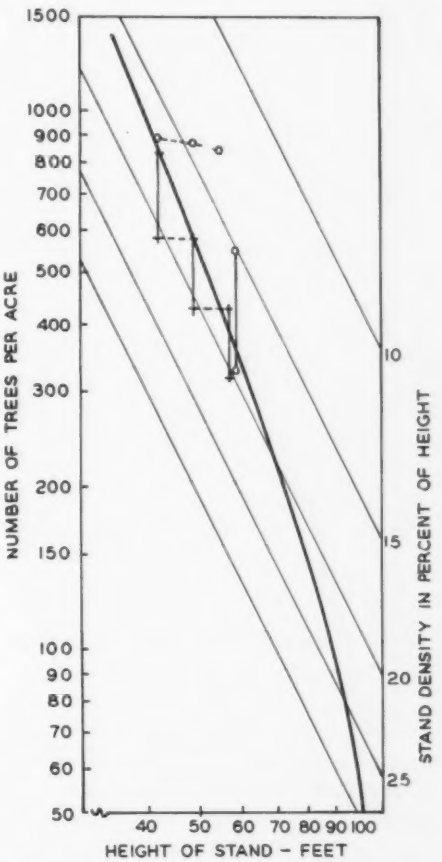

FIGURE 1. Stand density. Upper curve, Red pine check plot; stepped course, thinned plot; long curve, residual stand, Scotch pine, accretion thinning; vertical line at height 59 ft., second thinning of Monterey pine at age ten years.

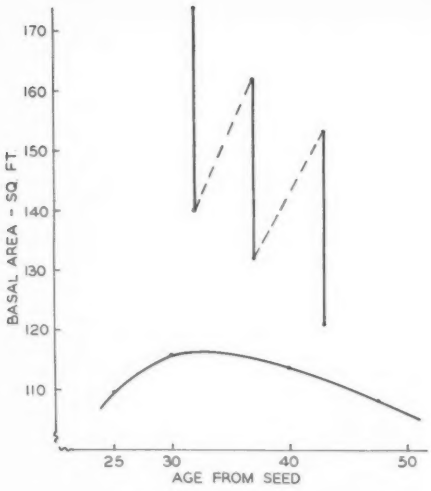

FIGURE 2. Trend of basal area. Upper, course of red pine thinned plot; lower, Scotch pine, residual stand after accretion thinning.

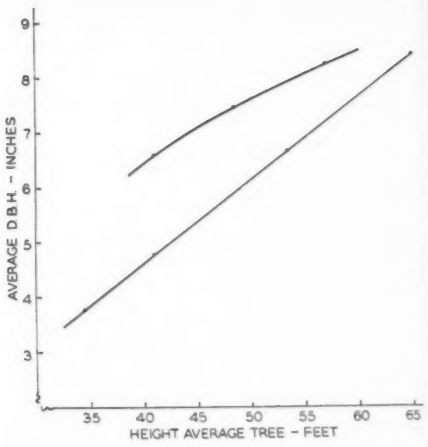

FIGURE 3. Trend of d.b.h. for average tree in residual stand. Upper, red pine thinned plot; lower, Scotch pine, accretion thinning.

While the data for Fig. 4 are inadequate for a statistical test, the correlation, in contrast to the vagaries of basal area, warrants further use and evaluation of Lexen's contribution. Only this sheath of stem cambium lays on merchantable wood. Like total volume, total bole area is based on all four factors: diameter, height, form, and number of trees; but expresses surface instead of contents.

Stand Density and Volume Increment

The similar increment in peeled cubic volume for the two red pine plots, despite increasing difference in stand density, indicates that thinning has not been so heavy as to reduce increment. The same volume growth per acre has been concentrated on fewer stems by thinning, another case in support of the increasingly accepted concept that volume increment is constant within certain wide limits of stand density.

In a period of forest depletion it was natural for European foresters to advocate full stocking for maximum increment, but after this was generally achieved the trend has been the other way. The current cut on the Schifferschaftwald in Baden is 9/10 growth and 1/10 reduction of growing stock. Wiedemann (1951), in referring to the shift from normal yield tables, states that light thinning to maintain normal full stocking was adhered to in many districts well into the present century. Since 1890 an increasing number of progressive foresters have turned to moderate thinning, while now heavy and even accretion thinning have become common practice. He points out that normal yield tables carry a background implication which silently promotes the thought that foresters should strive for full stocking, and claims complete freedom from the normality concept for his own tables.

Financial Returns from Thinning

While heavier thinnings negligibly affect total yield, they do change the proportion of early cuts and final harvest. Computation, using average price of land and ac-

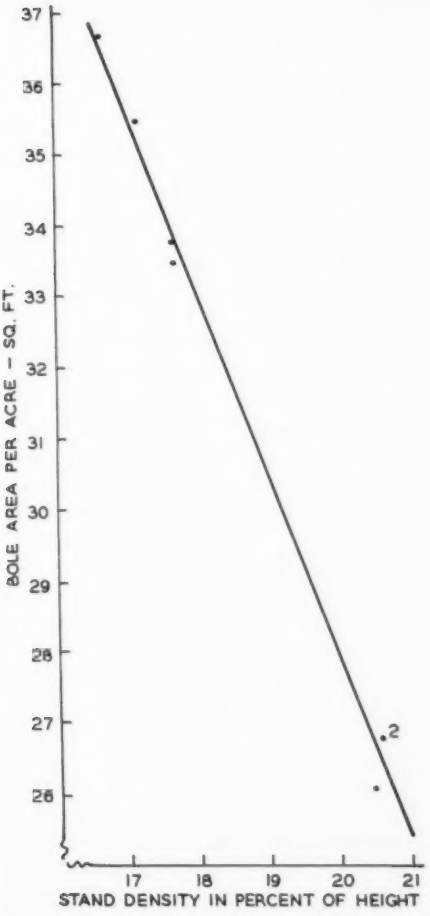

FIGURE 4. Bole area for check plot at first measurement, and for thinned plot before and after three thinnings.

tual planting cost, with annual taxes of ten cents per acre under the Wisconsin forest tax law plus another five cents per acre annually for supplemental protection, all carried at 3 percent compound interest, gives the present investment in the Star Lake check plot as $31.14 per acre. Due to a good market for pine pulpwood, the present value of net returns from the three thinnings is $113.09.

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Lesions Associated With Pole Blight of Western White Pine

BY
CHARLES D. LEAPHART
LAKE S. GILL

POLE BLIGHT IS A DISEASE of unknown origin affecting pole-sized western white pine (*Pinus monticola* Dougl.). This disease is characterized by a yellowing of foliage, a reduction in terminal and radial growth, bole lesions often associated with resinosis, and a general reduction of vigor (Anon., 1949; Wellner, 1947). Blighted trees appear to die from the top down. The yellowing, thinning, and dying of foliage progress until the tree succumbs. With one possible exception which has been reported but not entirely confirmed, trees once affected do not recover.[1]

Lesions have been regarded as important symptoms of pole blight. They are necrotic streaks in the bark and sapwood of the boles of affected trees. The streaks may range in length from several inches to over 20 feet and in width from a fraction of an inch to several inches. The sapwood beneath lesions becomes infiltrated with resin in varying degrees. Blue stain may occasionally be present in the killed sapwood. Some lesions may show evidence of callusing, but apparently its occurrence is rather exceptional.

Other features such as resinosis, "white face," flat face, etc., are often associated with lesions; these are discussed later.

[1]Hubert, Ernest E. (Ed.). Pole blight research progress reports. Univ. Idaho Coll. For. December 1953. (Mimeographed.)

Buchanan and his coworkers (1951) considered lesions to be invariably associated with the pole blight. They also stated that deterioration of the crown is correlated with both the degree of girdling and the relative area of necrotic cambium caused by lesions.

Gill *et al.* (1951) and Parker (1953) suggested that a fungus, *Leptographium* sp., may be the cause of necrosis in pole blight. Inoculations have shown that this fungus is pathogenic, but in a 5-year period trees inoculated with this fungus have not developed the symptoms of pole blight. Furthermore, the lesions produced by artificial inoculations show differences from the pattern of those found in nature. Hubert (1953) considered that *Leptographium* sp. is not directly responsible for the death of blighted trees. Unpublished observations subsequent to the inoculation study described by Gill, Leaphart, and Andrews tend to support Hubert's conclusions.

Among the first to make detailed studies of pole blight were John Ehrlich and Loren K. Baker. In a report (1942) to the U. S.

The authors are Forest Pathologists at the Intermountain Forest and Range Experiment Station and the Rocky Mountain Forest and Range Experiment Station, respectively. Both stations are research units of the Forest Service, U. S. Dept. of Agriculture. Thomas E. Hinds assisted in collecting field data and in taking photographs.

Forest Service and the University of Idaho School of Forestry, they stated that the diseased trees on the Coeur d'Alene and Kaniksu National Forests showed marked reduction in both radial and terminal growth. The reduction occurred either prior to or during the period of decline. In 1947 D. S. Welch reported to the same institutions that in 13 out of the 19 diseased trees he studied, the lesions originated before growth reduction. In the remaining 6, the lesions either followed or were concurrent with growth reduction.

The study reported here was undertaken primarily to verify Welch's findings, since all of his observations were made on a single 0.1-acre plot. If lesions originate before growth reduction, it would suggest that they might be primary in causing the decline and death of blighted trees. If more extensive study showed that lesions generally follow growth reduction, it would suggest that they develop only after the tree has suffered from some other disturbance. This in turn would tend to confirm the results of inoculation studies which thus far indicate that *Leptographium* sp. is probably not the primary cause of pole blight.

Methods of Study

During the summers of 1951 and 1952, 60 white pines were cut and studied on 6 selected areas on the Coeur d'Alene, Kaniksu, and St. Joe National Forests in northern Idaho. Fifty-one trees were in diseased areas and exhibited various degrees of health ranging from apparently blight-free to advanced pole blight. Nine healthy trees were included from 2 areas (Coeur d'Alene and Kaniksu National Forests) where pole blight was not present.

Descriptive notes and measurements together with disease classification were made on the selected trees while they were standing. Immediately after a tree was felled, additional measurements and notes were taken on terminal growth, total height, needle length, and needle color. The felled tree was then limbed and cut into 5-foot bolts which were oriented by nails driven along a tapeline stretching from the tip of the tree to the butt cut. Two-inch wafer specimens were cut at the 5-foot intervals for later study. The origin and extent of resinosis was also recorded for each bolt. The bolts were then peeled. Diagrams outlining the boundaries of lesions, flat faces, diseased but living bark, "white faces" suggesting an incipient pathological condition, and resin pockets were drawn to scale following the principles described by Buchanan *et al.* (1951). Additional wafer specimens were taken for the purpose of determining the age and progress of lesions and making other supplemental studies.

Wafer specimens were air-dried, resawn, sanded, and polished to a smooth surface for detailed study in the laboratory. Measurements and other determinations relating to radial growth and annual rings were made with the aid of a binocular dissecting microsope. The records included date of lesion origin, last year of growth showing no abnormal reduction or irregular growth, average annual growth over the last 25 years by 5-year periods, maximum girdling effect of lesions, and other data.

Periodic growth was recorded as the average of measurements on eight radii 45° apart, on a section 5.0 feet from the butt.

The last year of unaffected growth (LYUG) at any height was designated as the outermost annual ring in which no irregular or reduced growth occurred and continued in any portion of subsequent rings. To illustrate, in Figure 1A growth is noticeably irregular in 1946, 1947, and 1948. The 1949 ring is reduced in its entirety while all the subsequent rings are exceedingly narrow. In Figure 1B the wafer specimen, taken 60 feet below that in 1A, exhibits the sharp reduction in growth characteristic of blighted trees. The year 1945 was again selected as the LYUG because reduction started in a portion of the 1946 ring not shown in the photograph.

Lesions were considered as having originated in the year in which cambium was first killed.

Maximum girdling effect was determined by the same method Buchanan and his associates (1951) used in their study of pole blight symptoms. It was expressed as a percentage of the circumference at the level of maximum girdle.

Of the 60 trees used in the study, 22 were classified as healthy and 13 of these stood on diseased areas. For quantitative analyses only healthy trees on diseased areas were considered. One such healthy tree was discarded because of excessive age (120 years) and 1 diseased tree was not used because growth measurements at 5.0 feet were not available. The 9 trees from uninfected areas showed none of the abnormal conditions observed in trees from diseased stands. For most purposes, therefore, the sample included 49 trees, 12 of which were healthy and 37 diseased. Ages at stump height ranged from 49 to 75 years, about 60 percent falling in the 60- to 70-year age-class.

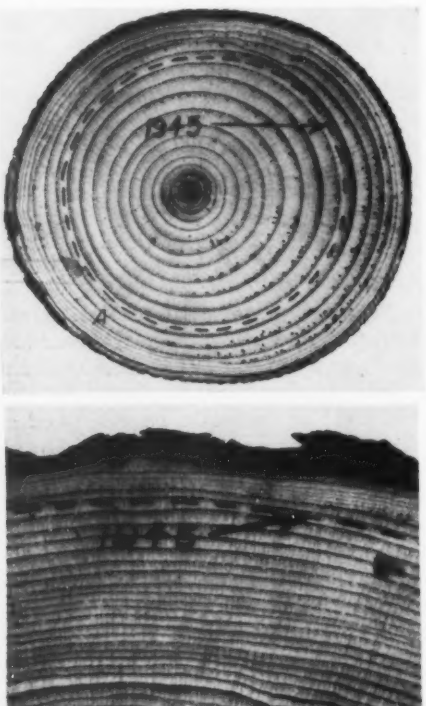

FIGURE 1. Growth reduction in a blighted pine. A, *Section taken approximately 17 feet below the tree top.* B, *Section taken 60 feet below* A. *The 1945 annual ring is considered for both* A *and* B *to be the last year of unaffected growth (LYUG).*

Results

Lesion Pattern. Four conditions were commonly encountered on the boles of blighted trees; lesions or necrotic cambium, necrotic bark, flat face, and white face. In the majority of cases, the lesions were confined to the lower half of the bole although some were in the upper part of the crown, others near the ground. Generally they are quite narrow compared to their length. In all cases, partial bark necrosis bordered the lesions.

Flat face is an inconsistent feature of both blighted and healthy trees. No relationship could be found between the presence of lesions and flat face. If the tree grows for a sufficiently long period after lesions originate, they will cause flat faces. Flat faces may form on white pine stems for no apparent reason, however, and normal healthy trees may outgrow them in a comparatively short period of years.

White face, observed for the first time in this study, is a condition found on freshly peeled sapwood and appears as an abnormal bleaching of the surface of the normal pinkish-yellow wood. White face was present in all trees classified as blighted or suspected and in 8 of the 12 healthy ones from blighted areas. This condition was not encountered in any of the healthy trees from healthy areas. The white face was often associated with the lesions on diseased trees. It usually surrounded the necrotic areas, and like them, ran parallel to the grain. On two trees, however, the white face was not associated with the lesions, which were small and showed evidence of healing. No histological studies of white face were undertaken in the present study.

In the majority of cases, lesions were not associated with knots or dead branch bases. When lesions appeared to develop around knots, they were usually less than a foot long. Lesions were not found in connection with live branch bases.

Resinosis usually occurred over or along the edge of areas of necrotic cambium, although sometimes lesions occurred without resinosis and vice versa. White pine will bleed profusely from a very small wound or bruise, and resin can often be encountered on healthy trees for no apparent reason.

Lesions are usually quite narrow compared with their length, as previously stated. Most of the longitudinal growth appears to take place within a comparatively short time, 1 or 2 years, after which it progresses much more slowly. One lesion elongated 17 feet in the year it originated; one directly above it extended 10 feet in 2 years. The variable rate of tangential spread of lesions, determined by the arc of cambium killed in a single year, is illustrated in Figure 2. In 6 years the left-hand lesion had spread around the circumference of the tree a total of 6.6 inches, whereas the right-hand one had spread 0.7 inch in 3 years.

Comparison of lesion dates plotted on complete tree diagrams suggested that lesions originating about the same time tend to merge. Tangential merging of lesions is apparently less common.

Typical pole blight lesions rarely callus. In contrast, those produced by inoculations with *Leptographium* sp. on healthy trees usually start to callus within 1 year,[2] becoming completely covered in time (Fig. 3). When callus develops on natural lesions, it is usually limited to the older ones, *i.e.*, those that originated while the tree was relatively vigorous. Lesions originating after the trees had reached an advanced stage of disease did not develop callus.

[2]Hubert, Ernest E. (Ed.). Pole blight research progress reports. Univ. Idaho Coll. For. October 1951. (Mimeographed.)

Relation of lesion origin to reduced growth. Sharp reduction in both terminal and radial growth occurs in blighted trees. The extent and nature of radial growth reduction is not easily determined without using a microscope, because several outer rings are often so narrow that they could be mistaken for 1 year's growth. According to Haig (1932), diameter increment in normal white pine on a comparable site gradually decreases uniform for each decade through age 80. The growth rate of most of the healthy trees in this study gradually decreased, except for an upsurge of growth during the 6- to 10-year period prior to collection.

Reduction in both terminal and radial growth in the tops of trees usually lagged behind radial growth reduction at the 5-foot level. The LYUG (last year of un-

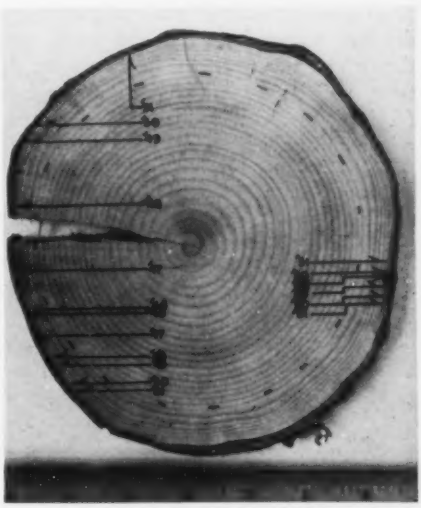

FIGURE 2. Tangential spread of pole blight lesions. Arrows mark the limits of annual ring growth and the yearly spread of the lesion killing the cambium. Lesion on the left started in 1945; the other in 1948. Annual ring for 1940, last year of unaffected growth, is marked by dashes. Serious retardation of growth began in 1943. Collection made in 1951.

affected growth) of the leader was taken as the year preceding the first year of continuing subnormal growth. Determination of both rate of radial growth and LYUG in the top was made from a section taken 10 feet below the highest 5-foot bolt in the tree. In the top sections, the LYUG was an average of 3.2 years later than at 5 feet above the butt, whereas the lag in the growth of the leader was 3.5 years. Although these averages agree closely, they are based on wide variations as shown in Figure 4. For example, in 60 percent of the cases the interval ranged from 0 to 3 years, but at the other extreme 20 percent of the trees showed a lag of 6 to 13 years. In one of the 49 trees used in this study radial growth reduction at 5 feet followed terminal growth reduction by 3 years but was concurrent with radial growth reduction in the top section. This tree is omitted from Figure 4 along with 5 others which showed no reduction in growth.

In 3 of the trees shown in Figure 4, reduction occurred within the same year throughout the tree. In the remaining 40 trees, radial growth reduction at the base (5 feet) preceded reduction in both terminal and radial growth in the top. In comparing radial growth reduction in the top with terminal growth reduction, the differences were found to be less marked and somewhat more inconsistent. In 9 of the 40 trees, the two types of growth reduction coincided; in 23 they were from 1 to 2 years apart; and in 8 they were from 3 to 7 years apart. In 18 trees radial growth reduction occurred first; in 13 leader growth reduction occurred first.

Table 1 shows the distribution of the sample trees by disease classes and by degrees of girdling, as well as the growth during the last two 5-year periods prior to cutting. Certain trends are indicated in the table. First, lesions tend to be more severe in trees with advanced than with suspected stages of disease. Second, lesions occur in all diseased trees except perhaps a few in the earliest stages of pole blight. Third, growth reduction during the last 5 years is increasingly pronounced as disease severity increases. The difference in growth between the last two 5-year periods follows the same trend. Fourth, growth reduction during the last 5 years is marked in all trees with lesions but shows no correlation with degree of girdle. However, the difference in growth between the last two 5-year periods appears to increase directly with the degree of girdle. Fifth, the most severely lesioned trees as well as those in the most advanced stages of disease were growing most rapidly in the period 6 to 10 years prior to cutting.

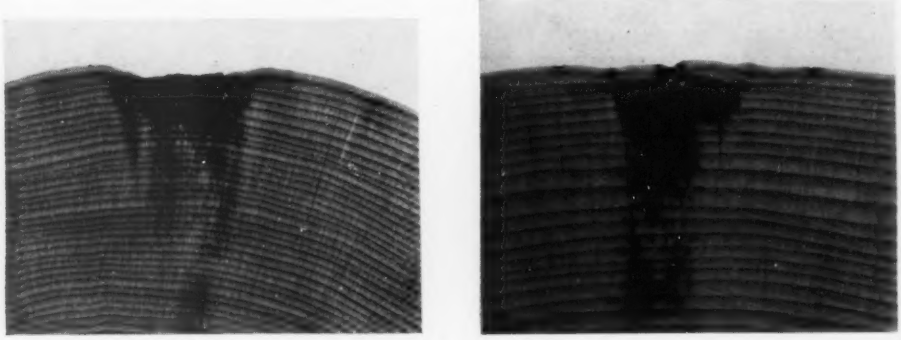

FIGURE 3. Callus of artificial lesions that resulted from inoculations with Leptographium *sp. on healthy trees.* A, *Partially callused 2 years after inoculation;* B, *3 years after inoculation.*

TABLE 1. Distribution of 49 sample trees by disease class and degree of girdle and periodic growth in percent of normal[1] for the 10 years prior to collection.

Fraction of circumference girdled by lesions	Healthy	Suspected pole blight	Definite pole blight	Growth—percent of normal		
				Period 0-5 years	Period 6-10 years	Difference
	(number)	*(number)*	*(number)*	*(percent)*	*(percent)*	*(percent)*
0	11	2	0	70	87	—17
Negligible	[2]1	7	2	44	76	—32
1/16 - 1/8	0	2	6	29	75	—46
1/8+	0	1	6	40	93	—53
1/4+	0	0	7	29	99	—70
1/2+	0	0	4	41	120	—89
Growth period:	*(growth—percent of normal)*					
0-5 years	74	49	30	-----	-----	-----
6-10 years	88	86	89	-----	-----	-----
Difference	—14	—37	—59	-----	-----	-----

[1]Normal based on Haig's normal yield table (1932) for second growth dominant and codominant white pines of the same age and on identical sites.

[2]Lesions on this tree were small and callusing vigorously, hence may not be associated with pole blight.

Various relationships suggested in Table 1 were tested statistically for significance. These showed only that (1) growth during the last 5 years was significantly higher (1 percent level) in healthy than in diseased trees, and (2) degree of growth reduction and severity of the disease are positively correlated. The latter was determined by a correlation analysis in which arbitrary numerical values were assigned to descriptive disease categories. Tests of variance between disease categories showed no significant differences in growth reduction.

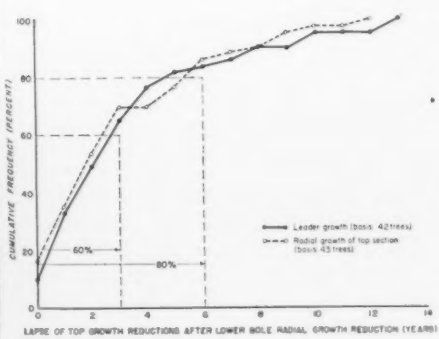

FIGURE 4. Distribution of 43 sample trees by comparison of the differences between growth reduction in the lower bole and in the top.

Marked growth reduction apparently is a characteristic and invariable condition associated with pole blight; lesion development and crown decline probably follow it at extremely variable rates of progress.

Excluding trees with no lesions, growth reduction occurred on an average of 4.3 years before lesions developed. Although the interval varied widely (Fig. 5), age of the oldest lesions on the trees was significantly correlated (at the 2-percent level) with reduced growth; the older the lesion, the longer growth had been retarded. In this sample, the correlation tended to be closer in those trees that were definitely

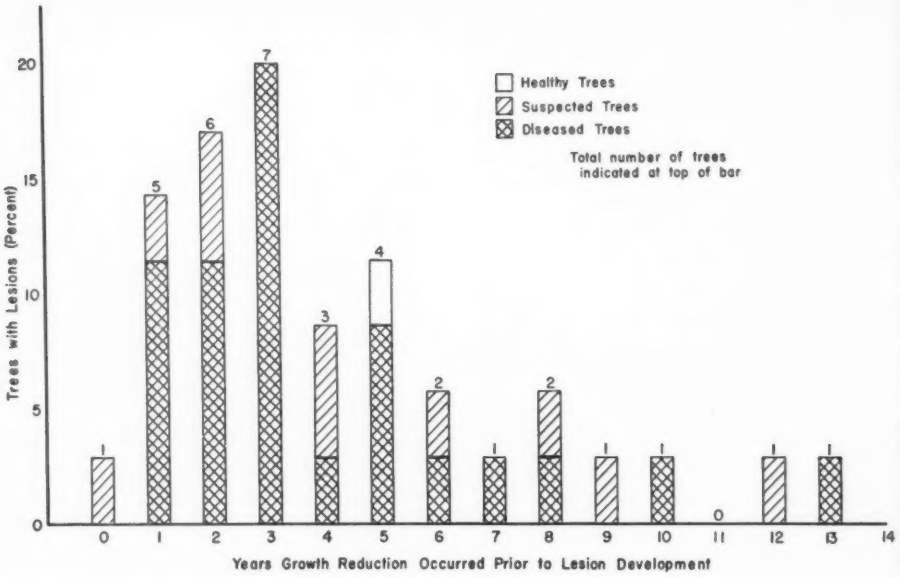
Healthy Trees
Suspected Trees
Diseased Trees
Total number of trees indicated at top of bar
Trees with Lesions (Percent)
Years Growth Reduction Occurred Prior to Lesion Development

FIGURE 5. Frequency distribution of 35 trees possessing lesions by disease class.

diseased; in the suspected class there was greater dispersion of the data. To illustrate the extremes, one lesion originated concurrently with growth reduction; in another tree growth became retarded 13 years before the origin of a lesion, which was 3 years old at the time of felling. The first of these 2 trees is exceptional in two other ways: (1) it was the only tree in which growth reduction at 5 feet occurred later than in the leader, and (2) it was the most severely girdled of all the suspected pole blighted trees. In no case did lesions precede growth reduction.

Discussion

The study reported here is indicative rather than conclusive. It suggests that reduced radial growth is always associated with pole blight and precedes both crown decline and lesion development. A marked reduction in radial growth of the lower stem usually occurs before crown symptoms of the disease appear. Although lesions are generally associated with pole blighted trees, they apparently are not directly responsible for the progressive decline of diseased trees.

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Composite Volume Tables

Composite volume tables for timber and their application in the Lake States. By S. R. Gevorkiantz and L. P. Olsen. U. S. Dept. Agric. Tech. Bull. 1104. 1955. 51 pp. Available from Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C. 25 cents.

REVIEW by Stephen H. Spurr

University of Michigan

The long-awaited Gevorkiantz and Olsen composite volume tables are intended for use with Lake States species. The authors are well qualified to provide this synthesis of volume information. The basic tables are for board-foot volume (both Scribner and International Rule), cubic-foot volume, and cordwood volume. Factors affecting the accuracy of the volume estimates are analyzed in detail and adjustment techniques are provided for use where necessary or desirable.

These tables are the practical products of eminently practical forest mensurationists and will undoubtedly find widespread use. From the scientific stand point, however, they leave much to be desired. Little or no factual justification for the choice of the basic tables is given, statistical tests of precision are few, and the new tables are not adequately compared with other alternatives. Relatively little attention or acknowledgement is given to the many years of detailed study of volume table construction carried on in Europe and even in the United States. The basic comparison with species tables is based on a potpourri of existing species tables without regard to whether or not these tables were properly constructed or based upon sufficient data. Furthermore, the principal test employed is the percent deviation from actual volume. Least-squares procedures of testing precision and standard error tests are seldom discussed. In at least one case, the assumption that the cubic-foot volume of all species grouped is equal to 42 percent of the volume of an equivalent cylinder, the rule-of-thumb is less precise or accurate than it could easily have been.

The Lake States approach is undoubtedly an improvement upon the mass of unrelated species tables currently in use. It will be widely adopted. It would be indeed unfortunate, though, if the appearance of these tables should result in their unquestioned acceptance or in the diminution of statistical analysis of volume problems. Rather, they should be accepted as a brilliantly conceived generalization that will be modified and improved as further research is carried on.

Tests of CMU for Forestry

BY

FRANK W. WOODS

CMU [3-(p-chlorophenyl)-1, 1-dimethyl-urea] has been intensively tested as a soil sterilant in the sandhills of west Florida. Studies at the East Gulfcoast Research Center have revealed that these lands probably cannot be forested with pine unless competition from both scrub oaks and ground cover is eliminated. The problem has more than local implications, for sandhill lands comprise a total of some 9 million acres in the southeastern United States.

CMU is a nonvolatile, slightly acid, grayish-white powder with a very low solubility in water (230 p.p.m). It has a relatively low mammalian toxicity and flammability and is not corrosive.

Usually applied to the soil, CMU is absorbed through the root system. Shallow-rooted plants generally require less of the chemical than deep-rooted ones. McCall (1952) has given an excellent description of CMU and its potentialities. It has been useful in controlling nut grass (Dotzenko and Whitworth, 1952), Johnson grass, bindweed, ironweed, Canada thistle, Bermuda grass,[1] centipede grass (Parris and Rodgers, 1954), and many other weed plants. Its reported vigorous action made it a candidate for testing on sandhills weed plants.

[1]Weed, M. B. 1953. "CMU," a new herbicide for sugarcane. Paper presented at meeting of Amer. Soc. Sugarcane Technologists, Houma, La., Feb. 5, 1953. 8 pp. (Processed.)

Methods and Study Site

The study was carried out on the Chipola Experimental Forest, near Marianna, Fla. Four blocks, each with ten 1/20-acre plots, were surveyed for living vegetation and subsequently treated with CMU in April 1953. Dosages varying from 0 to 37 pounds per acre were applied with a hand-operated garden syrayer. A red dye was added to facilitate uniform coverage.

Mortality and injury of oaks and pine seedlings was determined by actual stem count. Ground cover was surveyed by permanent line-spot transects, the individual spots being $2\frac{1}{16}$ inches in diameter. Results are based upon differences between pre- and post-treatment vegetation surveys.

Chemical determinations for residual CMU in soil were made according to the method described by Lowen and Baker (1952).

The study area was typical of much of the Florida sandhills. Turkey oak (*Quercus laevis* Walt.), bluejack oak (*Q. incana* Bartr.), and wiregrass (*Aristida stricta* Michx.) dominated in the scrubby vegetation. A few longleaf pines (*Pinus palustris*

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Mill.) were present; they ranged in size from seedlings to trees 12 inches d.b.h.

The soils on the study area are Lakeland deep sands, with rapid internal drainage and poor water-holding capacity. Organic matter averages 1½ to 2 percent in the upper horizons. Field capacity is usually about 6 percent, with a wilting range of 1½ to 2 percent. Exchange capacity runs about 1 to 2 milliequivalents. Annual rainfall is approximately 57 inches, and on better soils the monthly distribution would be considered good.

Effect on Vegetation

At a rate of 11 pounds or more per acre, CMU satisfactorily controlled oaks of all sizes (Fig. 1). Effects could be seen soon after the chemical was applied. On younger leaves, necrosis first appeared around the margins and moved inward until the entire leaf was brown. On older leaves, the necrotic areas were not localized around edges, but occurred in the center as well, giving leaves a mottled appearance. Oaks had several leaf casts before they died. The second and third set of leaves were usually malformed and dwarfed.

Many trees observed as moribund at the end of the first growing season after treatment died before the end of the second growing season. These plants showed typical CMU leaf injury even during the second year.

Roots of moribund oaks at the end of the second growing season after treatment were brownish and had signs of cell breakdown. Free water could easily be expressed from discolored areas. Roots of healthy oaks in untreated check plots were firm and white.

The chemical often killed trees with only a few roots projecting into treated plots. An oak 49 feet from the nearest plot (where the dosage had been 37 pounds per acre) showed signs of injury, lost its leaves, and died.

By the end of the second growing season, wiregrass was nearly eradicated and replaced by other grasses, including *Sorghastrum nutans* (L.) Nash, *Panicum virgatum* L., *Andropogon scoparius* Michx.,

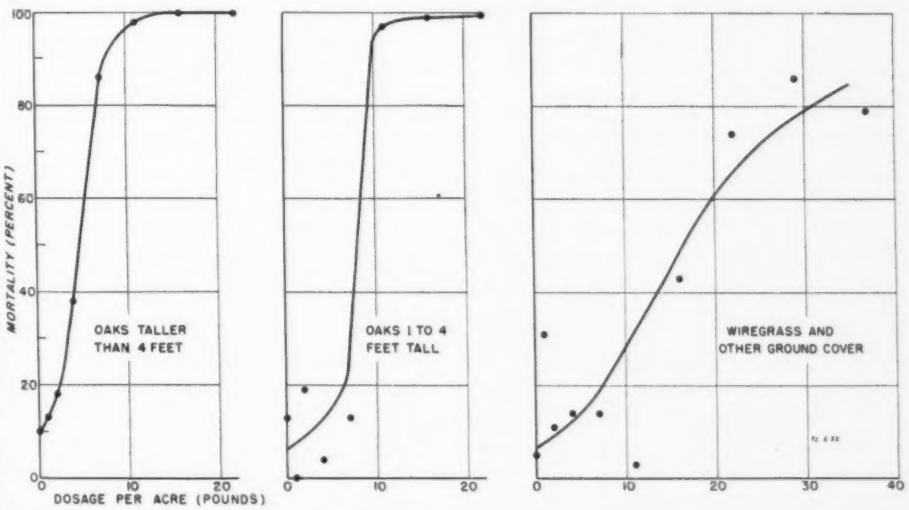

FIGURE 1. Mortality of oaks and ground cover at end of second season after application of CMU to soil.

and *A. floridanus* Scribn. Changes in composition were most apparent at dosages of ±7 pounds per acre. Lower rates did not kill much of the wiregrass, and very high dosages prevented the establishment of all plant life. The grasses that invaded treated plots were much taller and more vigorous than in untreated border strips. Wiregrass only 1 foot from treated plots was unaffected. The first apparent effect on grasses was yellowing of the tips.

CMU was not equally effective on all species of plants. Cactus (*Opuntia* spp.), saw-palmetto (*Serenoa repens* (Bartr.) Small), sassafras (*Sassafras albidum* (Nutt.) Nees), and yucca (*Yucca* spp.) exhibited a high degree of resistance. It has been shown (Haun and Peterson, 1954; Levi, 1955; Minshall, 1954) that CMU is translocated upward through the transpiration stream. It is reasonable, then, to expect species with lower transpiration rates, e.g. cactus, to be less affected by CMU than those with higher rates.

Pines of all age classes were killed but took much longer than the oaks to defoliate. So persistent were the needles that it was first thought a selective phytocide had been found. Not so: the rate of pine mortality was as high as that of other woody species. Pine needles, like the grass leaves, first turned yellow at the tips.

Persistence and Residual Effects

In January 1954, 9 months after application of the chemical, 49 slash pines were planted in each plot. A survival count in September of the same year showed that dosages as low as 4 pounds per acre had killed or injured 24 percent of these pines. Heavier dosages killed or injured up to 98 percent of the test trees (Fig. 2).

In July 1954, 15 months after application of the chemical, soil core samples were taken with a King tube from 3 soil depths (Table 1). CMU was found at all depths in all plots except the checks. The small difference in concentration between the 11- and 22-pound treatment is of interest.

TABLE 1. Residual CMU in soil 15 months after application

Soil depth sampled (inches)	Original dosages per acre		
	22 pounds	11 pounds	4 pounds
	(*p.p.m.*)	(*p.p.m.*)	(*p.p.m.*)
0–4	2.18	1.96	0.71
4–8	.81	.53	.11
8–12	.55	.27	.04

In another test, slash pines were planted on a site treated 24 months previously with 44 pounds of CMU per acre. Nine months after planting, 76 percent of these pines were dead or severely chlorotic. At the same time the pines were examined, sumac, French mulberry, cactus, grape, and blackberry plants on these plots showed signs of injury.

Hill *et al.* (1955) found that soil microorgansms play a role in the decomposition of the urea herbicides, of which CMU is one. The strong persistence of CMU is therefore indicative of low biological activity in sandhills soils. Loustalot *et al.*

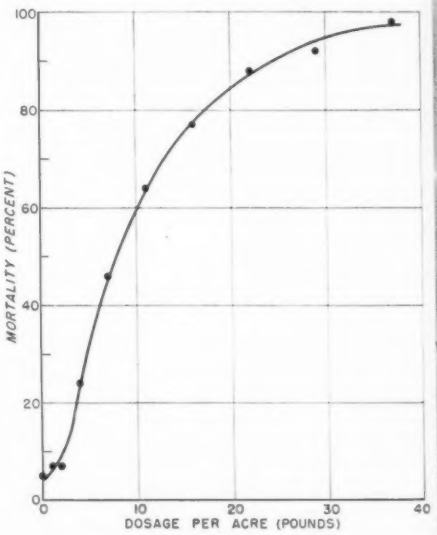

FIGURE 2. First-year mortality of slash pines planted 9 months after application of CMU to soil.

(1953) found that sandy soils retain CMU toxicity longer than clay soils; he attributed the cause to the greater microbial activity in the clay soils.

Summary

In the sandhills of western Florida, CMU killed scrub oaks at dosages of 11 pounds per acre. Much higher dosages were necessary to eliminate grass and other ground cover. During the second growing season after application, oaks continued to die although grasses generally held their own.

Composition of grasses and ground cover changed greatly in treated plots. The pretreatment dominant, *Aristida stricta*, was replaced during the second year by other grasses, including *Sorghastrum nutans*, *Panicum virgatum*, *Andropogon scoparius*, and *Andropogon floridanus*.

Slash pine seedlings planted 9 months after the application of the CMU were damaged or destroyed on all plots where the dosage had been 4 pounds or more per acre. Its persistence therefore renders CMU unsuitable for use as a pre-planting soil sterilant in sandhills soils.

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Seed Source Trials of Eastern White Pine

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EXTENSIVE NURSERY TESTS and limited field trials of a large number of collections of eastern white pine (*Pinus strobus* L.) seed at the Harvard Forest in Petersham, Massachusetts, provide information on the early development of this species as related to locality of seed collection, the tree from which the collection was made, and seed weight.

The objectives of the study were two-fold: (1) a provenance or seed source test to determine the extent of intraspecific variation of both local and distant sources by means of growing them together under uniform environmental conditions, and (2) an investigation of the possibility of identifying fast-growing strains in the nursery on the basis of their performance over a one- or two-year period.

The series of tests were initiated by Dr. P. R. Gast for the Maria Moors Cabot Foundation for Botanical Research, Harvard University, in 1937. Over a four-year period, two major nursery trials and several supplementary tests of white pine seed sources were carried on. The planning and execution of the experiments was done under the supervision of Dr. Gast to whom credit for the results obtained is due. One of the present authors (Spurr) was research assistant on the project from 1940 to 1942 and was responsible for much of the detail work and analysis of data.

The first nursery test involved the test of 86 collections from selected mother trees in the immediate vicinity of Petersham, while the second contained 94 seed sources from both local and distant localities. The Doe Valley nursery, containing the first test plants, was established in 1938 with seed from 1937 collections; while the Nichewaug nursery with the second was established in 1939 with seed collected in 1938 from New England, New York, Ontario, Michigan, Minnesota, and Virginia.

The supplementary tests included two series of pot cultures designed primarily to test the effect of various growth substances on selected seed sources, and a three-year test of the effect of seed weight on the early development of other selected sources.

In 1941 and 1942, individuals from 21 sources from each nursery were planted in field trials of approximately one acre each. These plantings were measured for the first time after the 1954 growing season by Frank Whitmore and assistants provided by the Cabot Foundation. At that time, Dr. Pauley, with the permission of Dr. Gast, made available existing data on the series of trials for final analysis and publication.

Experimental Design

The basic plan of all the trials was to plant

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seed of known weight and known seed source outside in the early spring. Each experiment was planned in accordance with a statistical design, balanced incomplete blocks being used for the two nursery and the two field trials. In the nursery, samples of the tops were cut following each of the first two growing seasons and their dry weights determined. In the field trials, stem diameter and amount of weevil damage was determined 13 years after establishment.

Statistical design. In the nursery trials, seed of a given origin were broadcast uniformly over a 1-foot section of a carefully prepared nursery bed 4 feet wide. In each nursery two series of balanced incomplete randomized blocks were used, the two experiments being laid down together in a checkerboard pattern. In the field trials the planting unit consisted of 16 trees planted in a square with a five-foot spacing between trees. Each of the two field trials consisted of a single series of incomplete randomized blocks.

The method of incomplete randomized blocks applied to field experimentation has been described by Yates (1936a, 1936b), while the modification adopted in the present experiments was developed by Youden (1937, 1940). This modification permits the construction of complete blocks of replicates without sacrificing the advantages of incomplete blocks. Furthermore, the blocks are sufficiently small that the field layout can be limited and site variation can thus be held to a minimum considering the number of varieties being tested.

The experimental design permits each variety to be replicated a number of times in such a manner that it grows once and once only in the same plot with every other variety. In determining the corrected yield, the total yield of each variety times the number of times it is replicated is compared to the total yield of the blocks in which that variety occurs. The resulting difference divided by the number of varieties represents the deviation of the yield of that variety from the mean of all varieties. If this deviation, therefore, is applied to the overall mean, the resultant value is the mean yield of the variety corrected for differences due to the variation in soil fertility between the blocks. Following the correction of variety means, the data were subjected to analysis of variance following usual techniques. The standard t test was used to test for significant differences between individual seed sources and groups of seed sources within the larger trials.

Nursery trials. The Doe Valley test was established in 1938 using seed collected in 1937. It was located on level glacio-fluvial outwash sand (Merrimack series) in southern Athol near the Petersham town line. The seed was collected from selected mother trees in five stands in the Harvard Forest and adjacent territory. Unfortunately, most of these trees were blown down in the 1938 hurricane. Two series of seed source trials were established, occupying the largest part of 19 nursery beds each 50 feet long and 4 feet wide. One series consisted of 57 varieties, each replicated 8 times; and the other of 31 varieties, each replicated 6 times. Top samples cut at the ground line were taken following each of the first two growing seasons. The better plants of 21 sources were selected for field planting after the fourth season.

The Nichewaug nursery was established in 1939 using seed collected in 1938. It was located on a level piece of glacial moraine (Charlton fine sandy loam) adjacent to the village of Petersham. Considerable effort was expended harrowing and fertilizing the tract to obtain as uniform site conditions as possible. The seed sources used represented 25 collections from Massachusetts, 27 from New Hampshire, 17 from New York, 21 from Ontario, 3 from Michigan, 9 from Minnesota, and 2 from Virginia.[1] Eight seed sources, previously tested in the Doe Valley nursery, were included in the Nichewaug tests, and ten seed sources were replicated in both series of the Nichewaug trials. Most of the col-

lections were from a single mother tree but nine stand collections were included. Two series of seed source trials, each consisting of 57 varieties replicated 8 times each, were established in a block of 21 nursery beds, each 50 by 4 feet in size. Growth was better than in the Doe Valley nursery. Top samples were cut at the ground line following each of the first two growing seasons. Selected varieties were planted in the field trials after the third season in the seedbeds.

Supplementary trials. In addition to the seed source tests in the nursery, a number of supplementary tests yielded information on some of the same seed sources and thus provided an opportunity to test the effect of different growing conditions on the relative growth of the different sources.

In two series of pot cultures (1940 and 1941) designed to investigate the effect of growth substances on the development of white pine seedlings,[2] ten of the seed lots that had previously been used in the Doe Valley trials were grown in washed quartz sand subirrigated with mineral nutrient solution.

In another experiment, 100 seeds of each of ten lots that had previously been used in the Nichewaug test were weighed individually and grown under controlled conditions (Spurr, 1944). Of these, one-third were grown in washed quartz sand in a hydroponicum subirrigated with mineral nutrient solution, while the others were grown in an artificial soil made up of equal parts of soil from the Nichewaug nursery, sand, and humus. In this test, records were kept for each individual seedling rather than for each lot as in previous experiments. After the conclusion of this three-year experiment, 12 trees of one seed source were left in the artificial soil bed for an additional five growing seasons to provide some idea of the lasting effect of seed weight upon growth.

Field trials. In May 1942, two plantations were established with seedling stock from the Doe Valley and Nichewaug nurseries. These plantings are situated on glacial till soil (Gloucester sandy loam) near the Quabbin Reservoir in the town of Hardwick, about one mile south of the Petersham town line.

Each plantation is approximately one acre in extent. The South Field was planted with 3-year-old seedling stock from the Nichewaug nursery, and the North Field with 4-year seedlings from the Doe Valley nursery. Each field was planted to 21 seed sources, each replicated 5 times. Each randomized incomplete block contained 5 seed sources, and each seed source was represented by sixteen trees in a square with a 5-foot spacing between trees. Extra plants were heeled in between regularly assigned points. Many lived, however, producing plots which had extra trees in 1955. Positions of blocks and of plots within blocks were randomly selected.

Planting was done in tilled strips plowed with a rotary tiller at 5-foot intervals in both directions. Each strip was plowed three times to a depth of eight inches in a strip 20 inches wide. The actual planting was done by digging holes about 16 inches in diameter and 12 to 14 inches in depth into which the seedlings were carefully placed. Roots were kept spread as the soil was added and gently tamped down.

It was originally intended to use both diameter and height as units in the 1954-55 measurements. Severe tip damage by the white pine weevil (*Pissodes strobi*), however, had so deformed the trees that height was eliminated as a usable measure. The number of weevilings per stem, therefore, was substituted. Diameters were taken

[1]Collections were made by the Cabot Foundation, New Hampshire Forestry and Recreation Department, New York State College of Forestry, Ontario Department of Lands and Forests, University of Michigan, University of Minnesota, and Tennessee Valley Authority.

[2]Gast, P. R., and S. H. Spurr. 1942. Adenine, B_1 and nicotinic acid and the growth of white pine seedlings. Unpub. ms. 19 pp.

TABLE 1. Effect of seed weight on first and second year top weight for seed from Petersham mother trees, Doe Valley Nursery.

Seed source	Year	Seed size class I	II	III	IV	V
		Dry weight (mg.)				
52 (Wilders)	rdw[1]	15.3	14.9	14.1	13.3	.....
	1938	101.5	93.2	85.3	82.3	.....
	1939	533	538	406	481	.....
10 (S.C. II-XI)	rdw	15.1	14.2	12.9	12.2	.....
	1938	96.5	87.1	83.3	79.6	.....
	1939	404	397	400	354	.....
50 (Wilders)	rdw	13.6	12.9	11.7	10.9	.....
	1938	73.9	65.6	64.9	58.0	
	1939	307	299	296	300	.....
20 (T.S. V-VI)	rdw	11.6	10.5	10.2	9.5	9.0
	1938	78.0	71.7	67.8	63.3	62.5
	1939	365	335	303	302	333
54 (Wilders)	rdw	9.8	9.4	8.4	8.1	5.5
	1938	62.7	57.9	55.5	47.6	46.2
	1939	300	265	255	204	227
11 (S.C. II-XI)	rdw	8.4	7.9	7.2	7.1	.....
	1938	54.5	52.0	46.1	51.9	.....
	1939	291	299	187	199	.....

[1]Reserve dry weight, or average dry weight of the seed less average dry weight of the seed coat.

to the nearest 0.5 centimeter at a height of 19.5 inches from the ground.

Seed Weight

In any effort to estimate growth of seedlings, the effect of seed weight must be taken into account. Large seed will produce large seedlings, small seed will produce small seedlings, and differences in inherent growth rate may well be masked by the effects of initial seed weight.

Gast (1937) and Mitchell (1934, 1937) have demonstrated that at any time during the first growing season, the size of the seedling is closely related to the weight of the seed and even more closely related to the "reserve dry weight" or "rdw," which is defined as the dry weight of the seed less the dry weight of its seedcoat. Furthermore, this relationship remains the same regardless of nutrient conditions. For example, if seed A is 10 percent heavier than seed B from the same tree, the plant resulting from seed A will be correspondingly heavier than that from seed B under any nutrient condition at any given time during the first growing season.

The effect of seed weight on the early development of eastern white pine was studied in detail over a 3-year period in one of the supplementary trials and the results have been published (Spurr, 1944). It was found that heavy seed germinated better, germinated earlier, and survived in a higher proportion than did light seed of the same source. Shoot weight at the end of the first year was closely correlated to seed weight. As the plants grew older, however, the effect of seed weight on shoot weight diminished, but was still highly significant at the end of the third year. This relationship was the same for all ten seed origins. Furthermore, the effect of seed weight on shoot weight was the same whether the plants were grown in a sand culture of high fertility or in a soil bed of moderate fer-

TABLE 2. Effect of seed weight on first and second year top weight for seed of all sources, Nichewaug Nursery.

Size class	No. of sources	Seed weight: Seed coat	Seed weight: rdw	Seed weight: Total	1939 (1 year)	1940 (2 years)
		Dry weight (mg.)				
Large	11	8.01	13.55	21.56	84.1	497
Medium large	20	7.74	12.24	19.98	75.5	465
Medium	33	6.93	10.69	17.62	67.7	434
Medium small	35	6.36	9.53	15.89	60.9	383
Small	15	5.67	8.00	13.67	50.0	314

tility. The effect of seed weight was independent of soil fertility and of seed source.

In a related study carried on at the Harvard Forest, Wright (1945) studied seed size from various portions of the cone in various parts of the tree. He found that the largest seed developed in the base of the cones on the largest cones of the tree. He found no obvious correlation between seed or cone size and the age, diameter, or growth rate of the parent.

The present paper presents data that antecedes the studies previously published and, in fact, provided the basis for their planning.

In preparing the seed for the Doe Valley trial, a seed sorting device was designed by Dr. Gast. The seed was placed in a vertical column and was subjected from below to an air blast. As the velocity of the air flow was increased, the seed rose higher in the column with the lower density seed being at the top. By drawing off successive fractions of the seed as the air velocity was increased, it was possible to sort large quantities of seed into approximate seed size classes.

The seed from six local origins was thus sorted into four to five weight classes, and each class was treated as a separate lot in the Doe Valley nursery. As Table 1 shows, the mean seed weight of each successive class was greater than that previously drawn off. Later, however, it was found by weighing several thousand individual seed on a micro-balance that the variance of seed weights within each class was great. While class I invariably had a higher mean weight than class II, the spread in individual seed weights within each class was several times greater than the differences between the means.

Notwithstanding, the Doe Valley data show a high degree of correlation between the mean reserve dry weight of the class and the dry weight of the tops at the end of the first year. After the second season, the relationship is still apparent, but the degree of correlation is much lower. The lesser correlation in subsequent years confirms on a larger scale the results obtained from the more precise small-scale tests.

In Table 1, the seed sources are arranged in order of decreasing seed weight. An inspection shows that seed from tree 20 was definitely faster-growing than seed from tree 50 inasmuch as its seed weight in each class is smaller but its corresponding top weights after one and two growing seasons are in each case larger.

Since the detailed study had shown that the effects of seed weight were independent of seed source, it was possible to sort the data from the Nichewaug nursery to demonstrate the effect of seed weight on early shoot weight on a large scale. All the sources were sorted into five broad seed-size classes, and the corresponding top weights were computed (Table 2). The plants from the 11 heaviest seed sources averaged 497 mg. top dry weight at the end of the

second season as compared to only 314 for the 15 lightest sources.

In the seed weight study, it had been found that a significant degree of correlation between seed weight and top weight was still apparent at the end of the third growing season, but that the effect was lessening from year to year. Twelve plants from a single seed origin (No. 10) were left in the artificial soils bed for an additional 5 years. At the end of eight growing seasons, these plants were measured, and the basal diameter, total height, and volume related to the actual weight of the individual seed from which they grew. No correlation was found, the effects of initial seed weight on growth having been apparently wiped out by variation in inherent growth capacity and by competition between the plants even though the site conditions were uniform. Omitting one badly-overtopped tree, the correlation coefficient between seed weight and 8-year volume was −0.204, a statistically non-significant value. Actually, the largest tree was the product of the smallest seed, and there was some indication that with a larger sample and wider spacing, the smaller seeds might be shown to produce larger trees.

Even though the effect of seed weight seems not to be very persistent, its importance for the first two years is evident. To determine growth differences between different seed sources, it is obviously necessary to take into account differing original seed weights. In the Doe Valley and Nichewaug nursery trials, this was done by computing an overall regression of seedling dry weight on reserve dry weight for each nursery at the end of each growing season. The following regression were obtained at the end of the first season:

$$\text{Doe Valley } Y = 17.21 - 4.78 \text{ rdw}$$
$$\text{Nichewaug } Y = 11.99 - 5.15 \text{ rdw}$$

where Y is the mean top weight of an oven-dried sample in milligrams, and *rdw* is the mean dry seed weight less the mean dry seed coat weight of a sample of seed taken from the seed source collection at the time of sowing.

From these and similar regressions, it is possible to adjust all yield values to a common reserve dry weight, thus correcting growth from the effects of differing seed weights.

Seedling Trials

In the two nursery trials, a total of 159 seed sources were tested over a two-year period. Of these, 148 were seed collected from single open pollinated mother trees, and 11 were mixed lots from a single stand. Geographically, 67 of the collections were from the town of Petersham, 13 were from other parts of Massachusetts, and 79 were from distant localities. From the standpoint of different nutrient levels, 15 seed sources were used in two separate trails; 4 were used in three trials, and 4 also in four trials.

The various trials are summarized in Table 3, together with the summary of the analyses of variance. Although adjustments for seed size were utilized in both the nursery trials, analyses of variance were run only for the first year of the Doe Valley trial.

Several basic conclusions can be drawn from this summary. First, the various seed sources differed significantly[3] in growth both on an unadjusted and on an adjusted (for seed weight differences) basis. There can be no question but that growth differences exist for eastern white pine between collections from single mother trees in a given locality and from mother trees in different localities. Where the analysis of variance is applied to unadjusted values, this significant variation is due in part to inherent growth capacity and in part to variation

[3]In this paper, significance is used in its statistical sense; non-significance denoting probabilities that differences noted are not due to chance are less than 1 out of 20, significance denoting probabilities greater than 1 out of 20, and high significance denoting probabilities greater than 1 out of 100.

TABLE 3. Summary of analyses of variance and seed source trials.

Experiment	Series and year	Seed size adj.[1]	Degrees of freedom	No. of collections	Mean yield[2]	Variance ratio (F)[3]	Std. error[4]
Doe Valley	H38	No	432	57	76.1 mg.	27.40 h.s.	3.3
	K38	No	180	31	71.5	17.05 h.s.	4.4
	H38	Yes	432	57	65.4 mg.	2.43	4.2
	K38	Yes	180	31	61.9	7.68 h.s.	4.5
Nichewaug	H39	No	420	57	407	17.13 h.s.	4.7
	K39	No	170	31	360	6.49 h.s.	7.2
	H39	No	453	57	68.8	105.03 h.s.	1.4
	K39	No	427	57	63.6	51.48 h.s.	2.0
	H40	No	451	57	421	9.79 h.s.	5.3
	K40	No	433	57	412	8.08 h.s	5.3
Pot cultures	40	No	159	8	84.0	24.73 h.s.	2.8
	40	Yes	159	8	----	12.35 h.s.	1.1
	41	No	----	7	121.3	----	----
	41	Yes	27	7	----	3.61 sig.	6.6
Seed weight	41	No	199	10	76.9	18.80 h.s.	5.6
	41	Yes	199	10	76.9	3.11 h.s.	4.2
North field	55	No	101	21	9.02 cm.	1.76 sig.	6.6
South field	55	No	91	21	8.07	1.76 sig.	7.5

[1] *Yes* indicates values adjusted to single *rdw*, or expressed on growth ratio basis.

[2] Mean top dry weight (*mg.*). Field trial yields are mean diameter (*cm.*), 19.5 inches from the ground.

[3] Ratio of variance between collections to error variance. *h.s.*, highly significant; *sig.*, significant.

[4] Expressed as a percent of the overall mean.

in seed weight between the different collections. The significant results obtained from adjusted values, though of a lower order than obtained from unadjusted values, demonstrate that inherent differences in growth rate do exist independently of seed weight variation.

In the trials that were carried more than one year, significance decreased with time. This fact does not necessarily indicate that variance between seed sources decreased, but rather that unexplained variance increased so that the resulting variance ratio (F) decreased with time. None the less, highly significant variation in mean top dry weights of the different seed sources was found after the second growing season in both the Doe Valley and Nichewaug nurseries.

In all cases, however, the error variance attributable in part to the variation in growing conditions within the individual trials and in part to genotypic variation within a given collection resulted in standard errors of from 1.1 to 7.2 percent of the mean yield. In the most precise nursery trial (Nichewaug, 1939), where site and growing conditions were most uniform, a difference of approximately 3 milligrams in mean top weight between two seed sources was necessary to establish significance by the *t* test. In the least precise trial (Doe Valley, 1939), where fertility differences in the nursery had affected second-year development, a difference of approximately 70 milligrams was similarly necessary. The former value is 5 percent of the mean yield while the latter is 18 percent of the mean yield. The large-scale nursery trials, therefore, are precise enough to classify a

given seed source as faster-growing than another given source only when the two seed sources vary by 5-18 percent depending upon the precision of the test. Smaller differences would of course be sufficient for demonstrating significance beween groups of seed sources.

In the supplementary tests, the standard error values are comparable to those obtained from the nursery trials. The number of seedlings of each source grown in the supplementary tests varied from 10 to 100, however, while the comparable numbers in the nursery ranged from 500 to 2000. It is evident, therefore, that the pot cultures and carefully-prepared artificial soils bed gave greater precision in the testing of the various seed sources. Even better results could be expected with more replications in the supplementary trials.

Coming to the individual trials, the Doe Valley nursery provides information on the growth of seed sources from various local stands in and near the Harvard Forest (Table 4). The three younger stands (designated by Compartments) had seeded in on abandoned fields on glacial till soils (Gloucester fine sandy loam), while the two older stands had come in on sandy outwash soils which had never been farmed. Although individual seed sources varied in their growth rates to a highly significant degree on both an unadjusted and adjusted basis in this trial, there is no evidence that this variation is correlated with the forest stands, its age, or the underlying soil type. In other words, there is no evidence of ecotypic variation in the Petersham white pine. We may, however, conclude that genetic diversity does exist in the Petersham white pine, but that such diversity is randomly distributed in what is apparently a single undifferentiated population of the species. This is to be expected for no barriers to cross-pollination are known to exist.

A different situation is encountered when other localities are considered as in the Nichewaug experiment. In Table 5, the seed sources are grouped by states or provinces. The Massaschusetts sources are subdivided into Petersham and other; the New Hampshire sources into southern, central, and northern groups; and the Ontario sources into peninsular or southern collections, Ottawa valley or northeastern collections, and central and western collections.

On the unadjusted mean top dry weight basis, the Virginia seed sources produced the largest seedlings during the first growing season, while the southern and central New Hampshire seedlings were the largest after the second season. No geographical trend is apparent from the unadjusted data.

When the adjustments for variation in initial seed weights have been made, however, a well-defined geographical pattern emerges. The local Petersham sources produced the largest 1-year plants while the other Massachusetts sources and the penin-

TABLE 4. Doe Valley seed source trials. Top weights after first and second growing seasons.

Locality	Age	No. of sources	Top dry weight (mg.) Unadjusted 1938	Unadjusted 1939	Adjusted 1938	Adjusted 1939
Tom Swamp V and VI	55	9	81.7	378	66.7	343
Wilder's Woodlot	55	19	73.4	373	63.9	373
Slab City II and XI	60	12	64.3	309	64.7	353
Tom Swamp IX	90	10	89.5	465	68.4	382
Tom Swamp IV	150	10	71.9	340	64.1	348
Others[1]		3	77.6	374	65.6	352

[1]Townsend and Carver, Massachusetts.

TABLE 5. Nichewaug nursery seed source trials. Average dry weights of tops in milligrams for first two years' growth. (1939-1940)

Locality	No. of sources		Unadjusted mean dry weight		Adjusted mean dry weight	
	State	Area	1939	1940	1939	1940
Massachusetts	25		61.7	406	64.7	444
Petersham		14	65.3	427	66.6	435
Other		11	57.1	379	62.3	456
New Hampshire	27		71.2	458	64.4	424
South		11	71.7	470	64.7	430
Central		6	70.8	472	65.2	441
North		10	70.8	436	63.7	406
New York	17		64.9	395	64.4	409
Ontario	21		61.8	404	60.8	421
Peninsular area		10	59.4	402	61.7	459
Ottawa Valley		7	70.5	444	61.0	412
Central and West		4	65.9	341	58.5	340
Michigan	3		52.0	298	58.7	402
Minnesota	9		72.9	408	61.6	365
Virginia	2		81.4	395	66.0	308
Mean			65.7	414	63.4	418

sular Ontario sources produced the largest 2-year plants. Keeping in mind the size of the experimental error, it is apparent that the local sources are best adapted. The farther away geographically and climatewise the collection is made, the poorer it does in the Petersham environment. Variation in growth rate between the sources from the different localities is not great, and there is no growth evidence or substantiating morphological observations to indicate the existence of well-defined ecotypes.[4] Rather, there is a clinical variation in growth behavior as would be expected for a tree which is common over a continuous range.

Even clearer evidence of the growth variation attributable to localities is given when the growth of the white pine is expressed in terms of *growth ratios*. This term is defined as the number of times the plant increased in dry weight during the growing season. The mean growth ratio for the first two years for the Massachusetts sources was 6.56, followed by 6.39 for New Hampshire, 6.29 for New York, 6.23 for Ontario, 5.89 for Michigan, 5.78 for Minnesota, and 5.60 for Virginia. On this basis, there is continuous decline in growth rate from Massachusetts north and west, and even greater decline for the southern Virginia collections. All differences proved highly significant by analysis of variance and subsequent t test.

In the course of the various trials, the seedlings were grown under various fertility levels. During the first year, growth in the Nichewaug and Doe Valley nurseries was comparable. The mean top dry weight of the 8 sources common to both nurseries was 70 milligrams for the Doe Valley and 65 milligrams for the Nichewaug nursery. During the second season, however, the poorer fertility and moisture conditions of the Doe Valley resulted in a mean top-weight of 332 milligrams as against 421 for the Nichewaug.

Better growth, however, was obtained in the supplementary trials. The mean top

[4]In a later collection by Dr. Pauley, however, a 5-year-old collection from a North Carolina source is characterized by a distinctly bluish cast to the needles.

TABLE 6. Growth correlations of seed sources common to more than one trial.

Trials	Number of common sources	Correlation coefficient: Unadjusted values	Correlation coefficient: Adjusted values
Nichewaug and Hydroponicum, first year	10	0.955 h.s.	0.631 sig.
Hydroponicum and Artificial soils, first year	10	0.941 h.s.	0.381
Nichewaug and Artificial soils, first year	10	0.887 h.s.	—0.033
Nichewaug and Artificial soils, second year	9	0.763 sig.	0.066
Nichewaug and Doe Valley, first year	8	0.759 sig.	0.431
Nichewaug and Doe Valley, second year	8	0.077	—0.412
Doe Valley and Pot Cultures, first year	10	—0.124	0.388
Nichewaug, first year, and Field trials	21	—0.393	—0.384
Nichewaug, second year, and Field trials	21	0.106	—0.550 h.s.
Doe Valley, first year, and Field trials	21	—0.077	—0.091
Doe Valley, second year, and Field trials	21	0.383	0.221

weight of the 10 sources grown in the pot cultures was 80 milligrams as compared to 67 milligrams for the same sources in Doe Valley. Both values are for the first year. In the seed weight experiment, the first-year weight of the 10 sources in the hydroponicum was 86 milligrams as compared to 69 milligrams for the artificial soil and 61 milligrams for the same sources in Nichewaug. After the second year, the weight of the 9 sources left in the artificial soils bed was 832 milligrams or more than twice as great as the 393 milligram average for the same source in Nichewaug.

Differences in nutrition clearly showed up during the first growing season. The hydroponicum provided the best growth, followed by the pot cultures, the artificial soils bed and the two nurseries. It was in the second year, however, that differences become pronounced with a difference of 500 milligrams mean top dry weight between the hydroponicum and the Doe Valley nursery, a difference that would be even greater were the seed size correction applied. In trials involving fertility levels, it would appear to be best to allow the seedlings to grow at least two years, for the effects of differing levels of nutrition are much greater the second year than in the first.

The number of seed sources replicated in more than one trial was not great, varying from eight to ten in the various paired trails. None the less, significant correlations were obtained between the behavior of the same seed sources in paired trials in several instances (Table 6). The highest correlations were obtained for unadjusted top weights after the first year between the three most precise trials—the hydroponicum, the artificial soils, and the Nichewaug nursery. The simple correlation coefficients ranged from 0.887 to 0.955. Significant correlations were also obtained using unadjusted top weights for seed sources replicated in both the Doe Valley and the Nichewaug nurseries. Other comparisons involving the Doe Valley nursery, however, were not significant.

When adjusted top weights were used, thus eliminating the effect of varying seed weights, significant results were obtained only for the seed sources used in the Nichewaug and the hydroponicum tests. Other paired trials gave correlation coefficients approaching statistical significance, and there seems little doubt but that significant results might have been obtained had a larger number of seed sources been replicated, or had more seedlings of each seed source been grown. Growth rates characteristic of a given seed source apparently occur under a wide range of soil fertility levels. In

TABLE 7. Field plantings. 1955 diameter and weeviling data compared with nursery data by groups of seed sources.

Seed source group	No. of sources	Seed rdw	Second year top wt. (mg.) Adjusted	Second year top wt. (mg.) Unadjusted	1955 Mean diam. (cm.)	1955 Ave. no. weevilings per stem
NORTH FIELD—DOE VALLEY NURSERY						
T. S. V & VI	2	12.6	404	366	9.92	1.92
Wilder's	9	11.6	409	388	8.73	2.14
S. C. II & XI	3	10.3	356	381	8.44	2.07
T. S. IX	6	14.4	500	406	9.49	2.10
T. S. IV	1	9.9	374	402	9.46	2.22
Mean	21	12.2	425	391	9.05	2.10
SOUTH FIELD—NICHEWAUG NURSERY						
Massachusetts	8	9.5	445	458	8.70	1.81
New Hampshire	9	10.3	480	476	7.86	1.73
New York	1	8.6	400	490	7.74	1.74
Ontario	3	8.1	409	529	7.10	1.67
Mean	21	9.6	453	477	8.07	1.76

small trials, though, a carefully designed and controlled experiment is necessary to establish the correlation. A larger number of sources or a larger number of plants within each source should be grown under carefully controlled conditions to determine the extent to which growth rate and soil fertility levels are interrelated.

Field Trials

When measured in 1954-1955, the two field trials could not be classified as successful plantations. Survival was poor and the live trees had been rendered bushy by repeated killing of the leader by the white pine weevil. Nevertheless, the behavior of the different seed sources is in accordance with their early behavior in the two nursery trials.

Survival in both the North and South Fields is poor, being 52.6 percent in the North Field planted with local stock from the Doe Valley nursery, and 42.6 percent in the South Field planted with local and distant stock from the Nichewaug nursery. Survival is particularly poor in a depression in the west corner of the North Field, apparently the result of frost conditions. The chief cause of low survival, however, was the severe drought of 1941, the year of planting.

Survival is higher for the local sources than for the distant sources. Overall survival for the local sources is 52.6 for those in the North Field and 50.8 percent for those in the South Field. In contrast, the non-local or distant sources in the South Field survived at the rate of only 37.4 percent.

Because of the weevil damage, growth measurements were confined to basal diameter. Use of the balanced incomplete randomized block design in each trial permitted the adjustment of the mean diameters of each seed source to reduce the effects of site variation within the planting site. The procedure is the same as that described for top weights in the nursery.

The analyses of variance for the two nursery trials are summarized at the bottom of Table 3. After 15 years' growth of trees in the North Field and 14 years' growth in the South Field, the differences in growth between seed sources is significant at the 5 percent level.

When the seed sources are grouped according to stand and locality (Table 7), the results clearly parallel the earlier nurs-

ery trials. There is no evidence to indicate that local ecotypes exist. In the North Field, the mean diameters of the trees from each stand show no consistent variation with stand, stand age, soil type, or original seed weight.

The trees from distant sources, though, are definitely growing at a slower rate than those from local sources. The more distant the collection the poorer the growth. The 14-year-old local trees in the South Field have an average diameter of 8.70 centimeters as compared to 9.05 for the 15-year-old local trees in the North Field. The New Hampshire strains have a diameter of only 7.86 at 14 years, followed by 7.74 for the single New York collection and 7.10 for the three Ontario sources. These differences are highly significant according to the *t*-test except for the New Hampshire-New York comparison.

Poor condition of the field trials resulting from low survival and heavy weeviling make it improbable that a high degree of correlation would be found between the behavior of individual collections in the nursery and in the field. Such indeed is the case (Table 6).

Surprisingly, a highly significant negative correlation was found between the adjusted second year Nichewaug top weight and the mean diameter of the same sources in the South Field. In other words, the larger the mean weight of a seed source after two years, the smaller the diameter would tend to be twelve years later. The correlation coefficient is not large (−0.550) and the negative regression may simply be due to an over-correction in the seed weight adjustment in 1940. At the same time, it is interesting to note that negative regressions are indicated by several of the non-significant correlations summarized in Table 6 and by the correlation between 8-year-old volume and seed weight for the 11 trees carried over in the seed weight trial. The point warrants further investigation.

The field trials confirm over a 14-15 year period the more extensive 2-year nursery trials in showing eastern white pine to be a species which is relatively homogeneous in its biotype, and which fails to exhibit clearly-defined ecotypes, although it does clearly show a clinical variation in growth behavior. Unusually large and vigorous specimens are rare and mass selection of seedlings in the nursery seems to offer little possibility for the improvement of this species. The present study confirms the finding of Ellertsen (1955) who reported that only 9 "super-seedlings" had been chosen out of 3,758,000 seedlings in the T.V.A. nursery. None of these outgrew their average-sized controls.

Virtually all the dominant and codominant trees in the field plantings had been badly deformed by the white pine weevil. As is usual, the weeviling was more severe in the larger and more open-grown trees. There was no evidence that any given source had been weeviled more severely or less severely than the others when differences in size and spacing had been taken into account.

In Table 7, the average number of weevilings per tree is given for each group of seed sources. As in the case of the diameter values, weeviling does not appear to differ markedly between the collections from the five local stands. In the South Field, however, the local sources are weeviled the most, followed by the New York and New Hampshire strains, while the Ontario collections are weeviled the least. Since this trend closely parallels the mean diameters of the same groups, it is logical to conclude that the local trees are weeviled the most simply because they are the largest trees, while the Ontario are weeviled the least because they are the smallest. No evidence was found indicating genetic resistance to weeviling independent of tree size or exposure.

Summary

Tests of 159 collections of eastern white pine (*Pinus strobus* L.) over two years in two experimental nurseries, and of 42 of the same collections for 13 years after-

wards in two field plantings provide information on the early development of this species as related to locality of seed collection, the tree from which the collection was made, and seed weight. The tests were carried on by the Maria Moors Cabot Foundation for Botanical Research at the Harvard Forest, Petersham, Massachusetts, from 1937 to 1955.

Seed weight is the most important factor affecting the size of 1-year white pine seedings and must be taken into account before the growth rates of even 2-year-old seedlings can be determined. In a limited test, however, no residual influence of seed weight was found after 8 years.

The great majority of the collections were from individual open-pollinated mother trees. Individual collections varied in their growth rates to a highly significant degree, but there is no indication that such variation is correlated with local diversity in site. There is thus no evidence that local ecotypes, identifiable on a growth rate basis, are present in the Petersham area. No distinct ecotypic diversity based on growth rate was discernible among the various geographic sources studied. Rather, variation in growth rate suggests a clinical pattern. The farther the collection was made from the Petersham area, and the more diverse the conditions of climate and site, the poorer the seed source did in the Petersham area. Plants from local seed grew best, followed in order by New Hampshire, New York and Ontario, Michigan, Minnesota, and Virginia sources.

Limited replication of 23 seed sources in more than one seedling trial indicated that growth differences between sources probably persisted independently of soil fertility levels, although the evidence here is not conclusive. Two-year-old seedlings showed much greater response than one-year plants to different fertility levels, and it would be desirable to grow white pine seedlings at least two years in any test involving nutrition.

Evidence of genetic diversity in growth rate among individual Petersham white pine mother trees suggests that careful selection of both parents and their controlled interpollination will yield progenies of increased vigor. Such improvements, however, have little to recommend them until weevil-resistant strains are isolated or adequate weevil control methods are perfected.

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